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Sedimentary legacy of sockeye salmon (Oncorhynchus nerka) and climate change in an ultra-oligotrophic, glacially-turbid British Columbia nursery lake

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SEDIMENTARY LEGACY OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) AND CLIMATE CHANGE IN AN ULTRA-OLIGOTROPHIC, GLACIALLY-TURBID BRITISH COLUMBIA NURSERY LAKE

By

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Anadromous Pacific salmon (*Oncorhynchus* spp.) populations are strongly regulated by climatic regimes and human activities across numerous spatial and temporal scales. The carcasses of adults returning to spawn provide important marine derived nutrients (MDN) to freshwater and terrestrial ecosystems through multiple trophic pathways. Sockeye salmon (*O. nerka*) rear extensively in lakes and recent studies of sockeye nursery lake sediments in Alaska have used indicators of spawner density ($\delta^{15}N$) and algal production (fossil pigments and diatoms) to show that lake trophic status is often regulated by climate and harvest via MDN from adult spawners. However, the strength of these controls and the utility of the paleolimnological techniques for measuring them are not well understood for sockeye nursery lakes in coastal British Columbia (BC). We examined relationships between climate, harvest, sockeye population dynamics, and lake trophic status from 1958 to 2005 using $\delta^{15}N$, $\delta^{13}C$, C:N, and fossil carotenoids in a radioisotope-dated sediment core from Kitlope Lake, BC. This ultra-oligotrophic, glacially-turbid nursery lake has a large (~872 km^2) pristine catchment and historically high, but currently depressed, sockeye returns. Climate and fisheries data supplemented with local and traditional knowledge (LTEK) indicated that sockeye escapements were regulated by both harvest and climate over the period of record. The sedimentary record of Kitlope Lake indicated extremely high sedimentation rates, significant inputs of terrestrial organic matter and periphytic diatoms from the main tributary, and the lowest $\delta^{15}N$ yet measured in a sockeye nursery lake. Nevertheless, sedimentary $\delta^{15}N$, C/N, and fossil pigments were coherent with order-of-magnitude changes in sockeye populations prior to the mid-1970s, after which time escapements fell below management targets while air temperature remained significantly correlated with sedimentary proxies of lake trophic status. Proxy-inferred algal production fluctuated but generally increased throughout the sediment core, likely due to an increased growing season caused by a warming climate, especially in the past decade. Despite potentially elevated productivity due to climate warming, Kitlope Lake remains nutrient limited with a depressed sockeye salmon population. A substantial increase in annual sockeye escapement is required to alleviate nutrient limitation in this system and ensure that the abundant rearing habitat is fully utilized.

Acknowledgements

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Preface

This thesis was written as a professional paper that will be reduced in length and submitted for journal publication, with Jack A. Stanford (thesis committee chairperson, University of Montana) and Peter R. Leavitt (collaborator, University of Regina) as co-authors. I therefore used the plural voice throughout for the sake of future editorial efficiency.

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Introduction

Dynamic controls on Pacific salmon populations

The effects of climate change and anthropogenic disturbance on aquatic ecosystems have become a major focus in fisheries ecology over the past decade or so. In the North Pacific region of North America there have been variations in oceanic and atmospheric climatic patterns over interannual to interdecadal time scales (reviewed and synthesized in Francis *et al.* 1998; Mantua and Hare 2002). These regime shifts have been linked with changes in land air temperature and precipitation, streamflow patterns, and biological productivity in terrestrial, marine, and freshwater ecosystems as far back as 1600 A.D. (Beamish *et al.* 1999; Mantua and Hare 2002). Salmon populations in the Northeast Pacific have exhibited corresponding basin-wide interdecadal population fluctuations, primarily in association with the Aleutian Low pressure system and coastal sea surface temperatures (Beamish and Bouillon 1993; Mantua *et al.* 1997). Pacific salmon have been of profound economic and cultural importance for millenia (Glavin 2000; Ames 2003; Butler and O'Connor 2004) and the effects of these multi-scale climatic changes have had important social and economic consequences. Over the last century or so, salmon populations have declined or disappeared over much of their spawning range in North America (Gresh *et al.* 2000; Schoonmaker *et al.* 2003; Riddell 2004). In addition to the climatic trends listed above, the reasons for these declines include degradation and isolation of freshwater habitats and over-harvest coupled with ill-conceived hatchery supplementations (Nehlsen *et al.* 1991).

Pacific salmon accumulate over 95% of their biomass during the marine phase of their life cycles (Groot and Margolis 1991) and therefore transfer nutrients and energy from marine to freshwater and terrestrial ecosystems through multiple pathways when they return to their natal streams to spawn and die (Gende *et al.* 2002). The C:N:P ratio of salmon-borne nutrients is much lower than the Redfield ratio, making them particularly important in the many salmon systems where P and/or N are limiting (Naiman *et al.* 2002). Numerous researchers have used stable isotope ratios ($_{15}N/_{14}N$ and $_{13}C/_{12}C$) to document the vast influences that these marine derived nutrients (MDN) have on freshwater and riparian foodwebs (reviewed in Cederholm *et al.* 1999; Gende *et al.* 2002;

Naiman *et al.* 2002; Schindler *et al.* 2003). These studies have generally demonstrated that the maintenance of the productivity, richness, and diversity of freshwater and terrestrial ecosystems, including the productivity of salmon populations themselves, are dependent on annual pulses of MDN to lakes and rivers via spawning salmon.

In the case of sockeye salmon (*Oncorhynchus nerka*), lacustrine environments are particularly important as juvenile sockeye typically spend 1-3 years in lakes feeding primarily on pelagic zooplankton before going to sea (Burgner 1991; Quinn 2005). Temperate oligotrophic lakes are usually phosphorus limited or co-limited by phosphorus and nitrogen (Wetzel 2001) and mass balance studies have shown MDN to be a major net nutrient source for sockeye salmon nursery lakes (e.g. Donaldson 1967; Moore and Schindler 2004). Many ecologists have hypothesized that juvenile sockeye salmon production is therefore dependent on the seasonal MDN pulse to these lakes, and juvenile sockeye production has been hampered by reduced MDN inputs due to various combinations of habitat loss, overharvest, and unfavourable ocean conditions (Schmidt *et al.* 1998; Stockner 2003). In fact, the idea that sockeye nursery lakes are abnormally nutrient-limited due to the depensatory effects of overharvest and poor ocean survivals of adult spawners has been the justification for decades of artificial fertilization in these lakes and streams (Hyatt and Stockner 1985; Stockner and MacIsaac 1996; Shortreed *et al.* 2001; Stockner 2003).

Productivity of sockeye populations and their nursery lakes

Until recently it has been difficult, if not impossible, for researchers to rigorously estimate changes in individual salmon population sizes and the corresponding trophic status of sockeye nursery lakes prior to the introduction of commercial fisheries. Recent advances in paleolimnology have allowed researchers to reconstruct the past productivity of salmon populations and their nursery lakes using geochemical and biological proxies in radioisotope-dated lake sediments. Numerous studies in Alaska have recently demonstrated significant correlations between sockeye salmon spawner densities (fish per unit lake area) and $\delta_{15}N$ in zooplankton, sockeye smolts, and lake surface sediments (Finney *et al.* 2000; Barto 2004; Gregory-Eaves *et al.* 2004; Schindler *et al.* 2005a; Schindler *et al.* 2006; Brock *et al.* in press). In lakes where time-series sediments were

examined, these same researchers found that sockeye spawner densities were significantly correlated with $\delta_{15}N$, fossil pigment and cladoceran concentrations, and relative abundance of diatom indicator species.

The strong correlations demonstrated between known spawner densities and sedimentary indicators of MDN and primary and secondary production have enabled the use of isotopic mixing models to extend sockeye salmon escapement estimates back several hundred years beyond the earliest quantitative catch and escapement records (Finney *et al.* 2000; Finney *et al.* 2002; Schindler *et al.* 2005a; Schindler *et al.* 2006). Finney *et al*. (2000 & 2002) found remarkable coherence between their mixing model-based estimates of past salmon abundance and other proxy estimates of historic climate trends, corroborating the strong links between salmon and climate found among more recent data sets. They suggested that the ability of sockeye populations to rebound from periodic climate-forced depressions was hampered in the 20th century when the nutrient feedback cycle was interrupted by aggressive commercial harvest. Schindler *et al*. (2005a) found through their Lake Nerka, AK mixing model that although lowered escapements due to commercial harvest had substantially reduced lake primary productivity, overall returns (commercial catch + escapement) were not affected, suggesting other factors besides lake productivity were limiting to sockeye production. In other Alaskan lakes however, it was demonstrated that although MDN and sedimentary proxy-inferred aquatic primary productivity are generally correlated, the degree to which MDN flux controls primary productivity in a single lake can change over time with little coherence in trends between nearby lakes (Brock *et al.* in press).

Paleolimnological studies have vastly improved our understanding of the complex relationships between climate, harvest, lake trophic status, and sockeye salmon production. However, these studies were mostly conducted on large Alaskan sockeye nursery lakes with low flushing rates and relatively high spawner densities (Finney *et al.* 2000). Furthermore, all of the lakes included in time series studies so far were clear (transparent), except for one dystrophic lake (Packers Lake, AK: Gregory-Eaves *et al.* 2004) and none were glacially turbid. In contrast most coastal sockeye nursery lakes in British Columbia (BC) are oligotrophic or ultra-oligotrophic owing to very low inputs of N and P from their catchments, due to local geology, and may not retain nutrients as

readily as interior lakes, due to higher flushing rates from greater annual precipitation (Stockner 1987). In a study of three nursery lakes with high flushing rates and a range of spawner densities, Holtham *et al*. (2004) found very little correlation between sockeye escapements and time-series sedimentary $\delta_{15}N$ but found slight shifts in diatom assemblages that were associated with climatic changes and a lake fertilization program.

Of the three main categories of sockeye nursery lakes that have been described for the British Columbia coast – clear, dystrophic, and glacially turbid – only clear and dystrophic nursery lakes have had extensive limnological study (Stockner *et al.* 1993 and references therein). Regional time-series paleolimnological studies of all three lake types are also sparse. In a survey of surface sediments from 11 BC sockeye nursery lakes $\delta_{15}N$ and chitin-inferred algal $\delta_{15}N$ were significantly correlated with sockeye escapements (Brahney *et al*. 2006). However, of the 14 lakes in the above two studies, only one (Meziadin Lake: Brahney *et al.* 2006) could be considered glacially turbid.

Despite the fact that most glacially turbid sockeye nursery lakes have cold thermal regimes, shallow euphotic zones, and low plankton productivity, many of them have historically had large returns of adult spawners (Shortreed *et al.* 2001; Riddell 2004) and supported intensive commercial fisheries for over a century (Lyons 1969; Argue and Shepard 2005). Sockeye populations in these lakes over the last few decades have suffered declines ranging from moderate (*e.g.* Kitlope Lake) to precipitous (*e.g.* Owikeno Lake) (Harvey and MacDuffee 2002; Riddell 2004). Despite these declines they continue to be exploited through mixed stock fisheries. At the same time the federal Department of Fisheries and Oceans (DFO) has very few reliable historic escapement records for many of them (Riddell 2004). Cursory surveys used to estimate returns on some systems have been cut back or suspended in recent years, despite the fact that the majority of these have not been receiving target escapements and harvest of the stocks is ongoing (Harvey and MacDuffee 2002; Riddell 2004). Paleolimnological studies estimating historic sockeye escapements and attendant lake trophic status would therefore be of great benefit on such lakes where historic records are spotty and do not extend far, and where sockeye populations are not achieving target escapements.

Watershed-scale considerations for north coastal British Columbia salmon rivers

The consideration of spatial and temporal scales is fundamental in studies of ecological processes and crucial for successful ecosystem-based management (Levin 1992; Stanford and Poole 1996). While oceanic and atmospheric climatic regime shifts have been shown to affect Pacific salmon abundance at basin-wide spatial scales and decadal to centennial time scales (Mantua *et al.* 1997; Beamish *et al.* 1999; Finney *et al.* 2002), other basin-wide analyses covering the past few decades demonstrated stronger coherence among multi-stock survival rates and environmental variables at smaller spatial and temporal scales (Peterman *et al.* 1998; Mueter *et al.* 2005; Pyper *et al.* 2005).

Basin-wide studies of climate change impacts on salmon habitat quality have been far more inclusive of time-series data sets from large commercially important systems than from smaller systems of moderate commercial importance. This is in part due to the fact (mentioned above) that high-quality catch and escapement data are often lacking for such systems, making it difficult to construct statistical models with a reasonable measure of confidence. Unfortunately this is a common paradox in ecology. Relatively intact ecosystems often make the best candidates for long-term studies of processes and responses but long-term data sets are harder to obtain for the more pristine, less impacted ecosystems, precisely because they are more pristine and less populated by humans, and therefore less convenient to monitor. Occasionally it becomes necessary to sacrifice some quantitative certainty to take advantage of the inherent value of a remote study location.

On the mainland coast of British Columbia, salmon stocks from the Skeena and Fraser systems receive the vast majority of research and management attention. Between these two systems however, lies a vast expanse of primary watersheds. Those mainland watersheds north of Vancouver Island account for the largest concentration of unimpounded primary watersheds in the Pacific Rim and support over 2500 individual salmon runs (Harvey and MacDuffee 2002). Many of these rivers are heavily influenced by glacial melt during the late summer and fall spawning seasons yet studies of climate change impacts on glacially-driven rivers and associated lakes and salmon populations in the mid-latitude coastal temperate zone are virtually nonexistent in the literature (Melack *et al.* 1997; Schindler 2001; Tyedmers and Ward 2001). As climate warming progresses and glaciers retreat in the mountainous headwaters of glacially-mediated temperate rivers

we are seeing corresponding changes in both hydrological and ecological regimes that are expected to continue (Hauer *et al.* 1997; Melack *et al.* 1997; Moore and Demuth 2001; Hall and Fagre 2003; Clague *et al.* 2004). However, the ways in which we can expect specific watersheds to change are difficult to predict due to high regional variability among myriad predictor and response variables (Melack *et al.* 1997).

Climatic changes are affecting temperate lakes through increasing interannual variability in freeze-up and break-up dates with a general trend towards longer ice-free periods and increased thermal stratification during the growing season (Magnuson *et al.* 2000; Schindler 2001). As discussed above, and not surprisingly, this trend has been shown to increase the forage base for juvenile sockeye salmon in some lakes (Schindler *et al.* 2005b). However, the effects of climate warming on the trophic status of sockeye nursery lakes dominated by glacial meltwater have received little study in north and central BC coastal watersheds.

Study purpose

Given the above considerations, we had three primary objectives in this study. The first objective was to examine the influence of oceanic and local climatic patterns and commercial harvest trends on sockeye salmon dynamics in a glacially-mediated north coastal BC watershed. Second, we examined the extent to which climate and sockeye-derived MDN regulate primary productivity in this glacially turbid sockeye nursery lake. And the third objective was to determine whether the paleoecological methods recently used to reconstruct past productivity of sockeye salmon populations and nursery lakes in Alaska would be applicable to ultra-oligotrophic, glacially-turbid sockeye nursery lakes in coastal British Columbia. We pursued these objectives using time-series sedimentary proxies of lake trophic status (total carbon, total nitrogen, C/N ratio, $\delta^{13}C$, fossil pigments) and MDN ($\delta^{15}N$), along with sockeye escapement estimates and climate records supplemented by local and traditional ecological knowledge and archival information. For our study site we chose ultra-oligotrophic, glacially-turbid Kitlope Lake, BC, located within a large (2750 km^2), pristine watershed with historically high but currently depressed sockeye salmon returns.

Methods

Site description

Catchment

The glacially-fed, high-gradient (5.89 m km^{-1}) Kitlope watershed empties into Gardner Canal – a long (30 km), narrow fjord on the north coast of British Columbia (BC) at 53°15'N, 127°55'W (Figure 1). It is the largest catchment within the largest contiguous area of undeveloped coastal temperate rainforest watersheds on Earth. At approximately 2750 km^2, the Greater Kitlope watershed is thought to be the largest undeveloped coastal temperate rainforest watershed in the world (Travers 1991). The entire watershed was protected from any industrial development in 1994 as a 'Class A' Provincial park – the highest level of protection that can be given to Crown land in British Columbia. The Kitlope Heritage Conservancy is adjacent to the Fjordlands Recreation Area to the west and Tweedsmuir Provincial Park to the east, forming a larger contiguous protected area of over one million hectares. Its size, remoteness, protected status, and relative lack of proximate anthropogenic disturbance make the Kitlope an ideal location to carry out long-term baseline studies of ecological processes and responses. As such the watershed has been a study site for the Salmonid Rivers Observatory Network, a research program of the Flathead Lake Biological Station, since 2004.

The entire catchment is within the traditional territory of the Haisla First Nation, who manage the protected area in partnership with the BC Provincial Government through the Kitlope Management Committee. While there are no longer any permanent settlements in the Kitlope watershed, it was the ancestral home to the Henaaksiala people, who amalgamated with the Haisla to the north after their numbers were severely reduced by post-contact epidemics (Pritchard 1977; Barbetti 2005; Appendix A).

The climate in the Kitlope watershed is controlled by the moderating influence of the Pacific Ocean as well as the colder continental climate of the interior coast mountains from which it originates (Stockner *et al.* 1993). The topography is extremely steep, with several permanent glaciers at the headwaters (Figure 1). Daily temperature and precipitation data have been collected by Environment Canada since 1951 in the Kemano

watershed at a point located 46 km from Kitlope Lake (UTM 09U, 570670 m E, 5933986m N, elevation 87 m) and daily streamflow data have been collected for the Kemano River since 1971. These data are typically used as proxy measures for the Kitlope watershed, for which there are no long-term climate or stream flow data. Based on these data, mean monthly temperatures from 1951-2002 range between -12.6 and 21.4 °C. Average annual precipitation for the Kitlope watershed is estimated at approximately 190 cm, with a recorded 24-hour maximum value of 12.6 cm, and a yearly maximum of 244 cm (Environment Canada). River levels are highly variable, and changes of > 1 m within a 24-hour period are common during and after high-runoff events (A. Hill pers. obs.)

Kitlope Lake

Kitlope Lake is 10 km upstream of the Kitlope estuary, approx. 3-5 km above the furthest extent of tidewater, at an elevation of 13 m. The lake has a surface area of 11.9 km^2, a mean depth of 86 m, and a maximum depth of 140 m in the centre (Figure 1). The glacially-fed Tezwa River is the lake's main tributary and drains a catchment of ~ 872 km^2.

The lake is cold, weakly stratified, glacially turbid, mildly acidic, poorly buffered, becomes covered in ice most winters, and appears to be phosphorus-limited during most of the growing season every year (Table 1) (Stockner *et al.* 1993; Shortreed *et al.* 2001). The mean residence time of the lake is 0.49 year and the daily flushing rate of the surface layer is 15-250 % (Stockner *et al.* 1993). Lake levels can fluctuate > 2 m in 24 hours during and after high-runoff events. The phytoplankton, zooplankton, and bacterial communities of Kitlope Lake all exhibit extremely low densities, low biomass, and low species diversity compared with other BC and Alaska sockeye nursery lakes (Stockner *et al.* 1993). Chlorophyll concentration, primary production (Table 1) and juvenile sockeye size and density in Kitlope Lake are among the lowest measured for any large sockeye nursery lake in British Columbia (Simpson *et al.* 1981; Shortreed *et al.* 2001). Three-spine stickleback (*Gasterosteus aculeatus*), typically a major competitor of juvenile sockeye, have also been found to be small and sparse here compared with most other sockeye nursery lakes (Simpson *et al.* 1981).

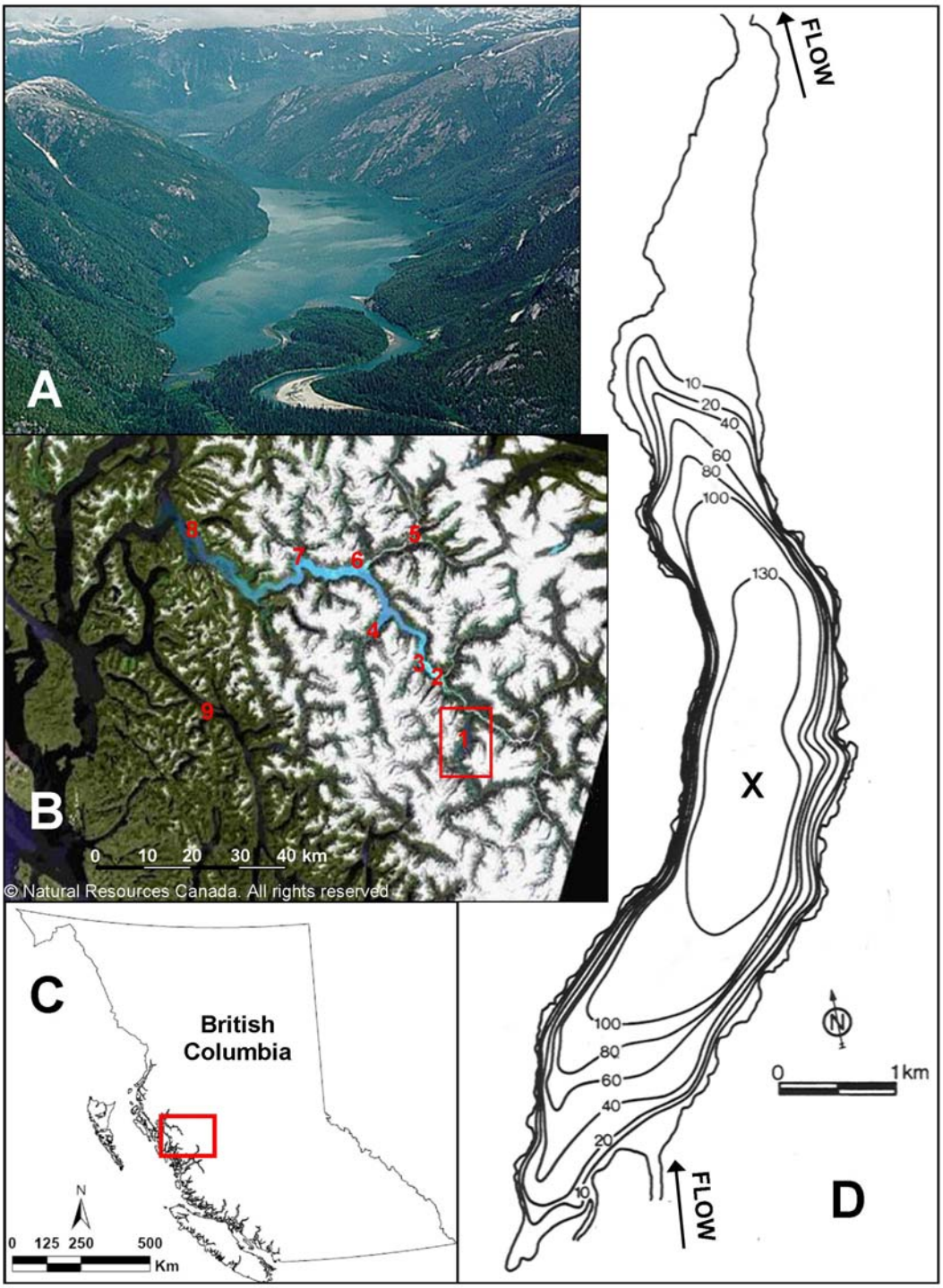

Figure 1. Kitlope Lake study area: (A) north (downstream) facing view of Kitlope Lake showing the inlet of the Tezwa R., the lake's primary tributary (photo by Myron Kozak); (B) Landsat image showing glacially coloured (bluish) Gardner Canal (centre), with Kitlope Lake (1), Kitlope estuary (2), Price Creek (3), Chief Matthews Bay (4), Kemano townsite and weather station (5), Kemano Beach (6), Brim R. (7), Crab R. (8), and Butedale (9) (image courtesy of Natural Resources Canada); (C) reference map; and (D) bathymetric map of Kitlope Lake (depths in metres), with the coring location marked by an "X" (Stockner *et al*. 1993 – map courtesy of Fisheries and Oceans Canada).

In order to boost sockeye production the federal Department of Fisheries and Oceans (DFO) fertilized the southern half of Kitlope Lake with aqueous ammonium nitrate and ammonium phosphate on a weekly basis for 18 weeks per year during the growing season from 1979-1983 and 1985 (1979-82: 7.67 mg P m^{-2} wk^{-1}, 50 mg N m^{-2} wk^{-1}; 1983 and 1985: 4 mg P m^{-2} wk^{-1}, 25 mg N m^{-2} wk^{-1}) (Stockner *et al.* 1993; Shortreed *et al.* 2001; Ken Shortreed, DFO, pers. comm.). A recent review of 60 BC sockeye nursery lakes by DFO limnologists identified Kitlope Lake as a good candidate for renewed fertilization regiments (Shortreed *et al.* 2001).

Table 1. General limnological information for Kitlope Lake. The 1978-80 data were based on weekly sampling through the growing season (Stockner *et al.* 1993); our 2005 data were collected on four sampling events (7/05, 8/02, 8/23, 9/26) for N and P and two additional sampling events (5/30, 6/18) for all other variables.

	1978 (Unfert.)	1979-80 (Fertilized)	2005
Total nitrogen (µg N L^{-1}):	--	--	121.4
Nitrate (µg N L^{-1}):			
Spring overturn	64	66	--
Mean epilimnetic	19	18	48
Seasonal minimum	6.1	8.0	--
Total phosphorus (µg P L^{-1}):			
spring – summer	1.5	--	7.1
late summer – fall	8.0	--	
Soluble reactive phosphorus (µg P L^{-1})	< 1	< 1	2.0
Chlorophyll (µg L^{-1})	0.56	0.60 – 1.10	0.96
Total alkalinity (mg $CaCO_3$ L^{-1})	1.6	1.5	--
Daily photosynthetic rate (mg C m^{-2})	54	65	--
Zooplankton biomass (mg dry wt m^{-2})	53	88	--
Euphotic zone (m)	7.6	8.6	9.7
Secchi disk depth (m)	1 – 6 m		1.3 – 4.2 m
Turbidity (NTU)	--	--	2.18
Seasonal average surface temp. (°C)	10.5		15.3
pH	6.22	6.10	6.46
Specific conductance (µS)	--	--	8.21
Drainage basin area:	872 km^2		
Lake area:	11.9 km^2		
Estimated average residence time:	0.49 years		
Estimated daily surface layer flushing:	15 – 250 %		

Salmon populations

The greater Kitlope watershed is inhabited by all 5 species of Pacific salmon; however, only sockeye, coho (*O. kisutch*), and chinook (*O. tshawytscha*), spawn in appreciable numbers upstream of Kitlope Lake in the Tezwa watershed, including Kalitan Creek (Rosberg *et al.* 1982; Cecil Paul Jr., Na Na Kila Inst., pers. comm.). Sockeye spawn in spring and mainstem channels in the river upstream from the lake, in the lake outlet river, and on several colluvial fans in the lake. The major interceptor of Kitlope-bound sockeye is the mixed-stock commercial fishery in DFO statistical area 6 near the mouth of Douglas Channel. Subsistence fishers from the Haisla First Nation take several hundred annually, and a large (~100) population of harbour seals (*Phoca vitulina*) prey on salmon throughout the watershed, estuary, and fjord during the migration and spawning seasons (Rosberg *et al*. 1982; Stockner *et al*. 1993; A.Hill pers. obs.; DFO unpubl.).

Data collection

Salmon escapements

Observations of sockeye run sizes in Kitlope Lake and its main tributary, the Tezwa River, have been recorded by DFO since 1921 based on boat and aerial surveys. Spawner escapement estimates from 1921-33 were made as simple qualitative rankings (i.e. light, medium, heavy). From 1934-84 estimates were made using pre-set categorical ranges of the total estimated number of spawners, as follows:

A. 1-50 B. 50-100 C. 100-300 . . . L. 20000-50000 M. 50000-100000 N. > 100000

From 1951-72 theses ranges were occasionally accompanied by specific estimates, and from 1973-83 all annual reports gave specific estimates. From 1984-present all reports have contained specific estimates only. Sockeye escapement estimates for 1950-2005 were obtained from the DFO BC16 database and from fishery officer reports from 1934-49 (Brian Spilsted, DFO, pers. comm.). For years where only categorical estimates were available median values were used for the analyses in this study.

Estimates of chinook and coho run sizes have only been made on occasional years, and these numbers are part of an aggregate escapement estimate for the entire Kitlope watershed, therefore it was not possible for the purposes of this study to derive

yearly escapement estimates for the portion of the Kitlope watershed upstream of Kitlope Lake. However, we can be reasonably certain that in most years sockeye comprised > 50 % of the salmon spawning biomass in and upstream of Kitlope Lake, based on the many years in which estimates were made of the coho and chinook escapement as well as Rosberg *et al*. (1982) and observations by field personnel over the past decade (A.Hill pers.obs.; Cecil Paul Jr., Na Na Kila Inst., pers.comm.).

Additional qualitative information regarding historic salmon abundance and harvest in the Kitlope system was gathered from several sources: cannery pack records from the Price & Co. cannery which was located near the Kitlope estuary from 1890-1893) (Lyons 1969); other archival sources (Lyons 1969; Newell 1989; Argue and Shepard 2005); and through local and traditional ecological knowledge (LTEK) from semi-directed interviews (Huntington 2000) with Haisla elders and others (Appendix A), and previously recorded Haisla traditional knowledge (Pritchard 1977; Barbetti 2005; unpublished Haisla archival notes).

Climate data

Daily and monthly temperature data from Kemano, BC 1951-2004 were downloaded from Environment Canada's website (http://climate.weatheroffice.ec.gc.ca/) and more recent data not available for download (2004-2006) were purchased from Environment Canada. Mean annual temperatures were calculated from mean monthly temperatures, and years with missing monthly values (1951, 1959, 1972, 1985, 1989-90, and 1993-94) were excluded or replaced with interpolated (5-point average) values for analyses. LTEK provided additional perspective on local climate change over approximately the past century (Appendix A).

Daily mean air temperatures from the Kemano weather station (Jan. 2004 – Jan. 2007) were graphically and statistically compared to daily averages of hourly air (July 2005 – Oct. 2006) and surface water (May 2004 – Oct. 2006) temperatures measured at the Kitlope Lake outflow using Vemco *Minilog-T* temperature loggers (UTM_{air} 09U, 581793m E, 5891274m N; UTM_{water} 09U, 582177, 5890940).

Pacific Decadal Oscillation (PDO) index values were downloaded from the University of Washington Joint Institute for the Atmosphere and Oceans (JISAO) website

(http://jisao.washington.edu/pdo/PDO.latest) for comparison with the Kemano temperature data, sockeye escapement estimates, and sedimentary proxies of lake trophic status.

Sediment collection

Sediment cores were collected by boat from Kitlope Lake on June 25-26, 2005. Three cores were taken from approximately the same mid-lake location (120 m depth; UTM 09U, 581530 m E, 5885879 m N; Figure 1D) after preliminary sonar readings from around the lake suggested that the lake's abyssal plain was large and flat enough to yield usable cores despite the high relief of the lake basin. A recent 74-core survey of Nerka Lake, Alaska demonstrated that a core from a single location should accurately record whole-lake nutrient flux and trophic dynamics (Brock *et al.* 2006).

Three sediment cores were collected by boat using a portable percussion coring device (Gilbert and Glew 1985) with 7.6 cm (3.0 in.) inside diameter Lexan® tubes (length: 2.0 m, fitted with brass shimstock core catchers (Reddering and Pinter 1985). The coring tube extended approx. 15 cm below the bottom of its aluminium struts so that it penetrated the substrate before the bulk of the coring device hit the lake bottom thus minimizing disturbance of the mud-water interface inside the core. The coring device was driven using a 22.7 kg (50 lb) hammer, and was suspended by a Kevlar® rope to facilitate a direct transfer of lift. The cores were extracted on a calm day in minimal wind (< 5 km/hr) with the boat nearly stationary so that the angle at which the device was driven into the substrate was near 90°. The cores were transported in an upright position to a field station approximately 10 km downstream from the collection site where they were immediately sectioned at 2.5 mm intervals using a vertical extruder (Glew 1988).

Sample handling and preparation

Samples were placed in Whirlpak® bags and immediately put on ice and in the dark inside a cooler, which was transported to the Flathead Lake Biological Station (University of Montana) in Polson, Montana. Each sample was then flushed with N_2 gas, resealed, and stored in vacuum-sealed bags in the dark at 4°C until processing.

The best of the three cores retrieved from Kitlope Lake was chosen for all analyses described henceforth except for diatom counts. This core (KI-C1, ~ 80 cm) was

chosen for its length, apparent lack of sediment mixing during extraction, and lack of gassing prior to extrusion compared to the other two cores. Whole sections were sequentially weighed, homogenized, and then partitioned for the various analyses described below. All subsample partitioning was done under minimal lighting to minimize photo-oxidation of fossil pigments. Subsamples for fossil pigments analysis were weighed into individual dark containers (black 35 mm film canisters), flushed with N_2 gas, sealed with black electrician's tape, and shipped frozen to the University of Regina Limnology Laboratory for analysis. Sediments for radioisotope and stable isotope analyses, as well as organic matter and bulk density measurements, were oven-dried at 60°C and stored in a desiccator until analysis. Random subsamples of the dried sediments were treated with concentrated hydrochloric acid (HCl) to test for the presence of inorganic carbon. No gas evolved from any samples upon HCl treatment and given the extremely low alkalinity values reported for Kitlope Lake (Stockner *et al*. 1993; Table 1) we assumed that sedimentary inorganic carbon concentrations were negligible. Given the low probability of carbonate presence and the fact that acid-washing has been shown to affect stable isotope ratios in young sediments (Meyers and Teranes 2001), we did not treat any samples with HCl prior to analyses, except for samples from core KI-C2 for diatom counts.

Sediment chronology

Sediment deposition dates were estimated by Flett Research Ltd. (Winnipeg, Manitoba, Canada) from down-core declines in ^{210}Pb activity using the constant rate of supply (CRS) model (Appleby and Oldfield 1978). ^{210}Pb activities were measured (via ^{210}Po) on 13 sections based on the methodology of Eakins and Morrison (1978) using an Ortec 'Octet' alpha spectrometer. All counting times were 60,000 seconds. Background ^{210}Po was estimated by measuring ^{226}Ra using ^{222}Rn emanation (Mathieu *et al.* 1988) on 3 deeper sections where ^{210}Po appeared to be above background levels.

Carbon and Nitrogen analyses

Samples for N and C analysis were placed in a random order and gently hand-ground with a mortar and pestle to break apart caked sediments but minimize breakdown of any terrestrial macrofossils that may be present. They were then dry-sieved at 250 μm

to remove terrestrial macrofossils which could confound the analysis, and weighed into foil capsules on a Sartorius M2P microbalance (precision 0.001 mg). Analysis was carried out on every section from 0 – 20 cm core depth, and every second section from 20 – 75 cm. Sample weights were large ($\bar{x}$ = 51.528 mg ± 1.00 mg std. dev.) to ensure elemental and isotopic measurements would be above detection limits. Stable isotope ratios of carbon and nitrogen were measured by continuous flow isotope ratio mass spectrometry at the University of California Davis Stable Isotope Facility (Davis, California, USA) using a 20-20 mass spectrometer (PDZ Europa, Northwich, UK) after sample combustion to CO_2 and N_2 at 1000°C in an on-line elemental analyzer (PDZ Europa ANCA-GSL). The gases were separated on a Carbosieve G column (Supelco, Bellefonte, PA, USA) before introduction to the Isotope Ratio Mass Spectrometer (IRMS). Sample isotope ratios were compared to those of standard gases injected directly into the IRMS before and after the sample peaks and $\delta^{15}N$ (atmospheric N_2) and $\delta^{13}C$ (Pee-Dee Belemnite limestone) values calculated. Final isotope values were adjusted to bring the mean values of standard samples distributed at intervals in each analytical run to the correct values of the working standards. The working standards are periodically calibrated against international isotope standards. Stable nitrogen and carbon isotope ratios were respectively expressed as:

$$\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000;\ R = {}^{15}N/{}^{14}N$$

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000;\ R = {}^{13}C/{}^{12}C$$

Coefficients of variation for checks (N = 37) done on the working standards for N, $\delta^{15}N$, C, and $\delta^{13}C$ were 1.22%, 11.87%, 1.70%, and 0.14%, respectively.

Organic carbon and nitrogen values were calculated as a percentage by weight and organic carbon to nitrogen ratios (C/N) were calculated as weight (not atomic) ratios.

Fossil pigments and sediment organic matter

Sediment organic matter content was estimated from percentage weight loss on ignition (LOI) for subsamples of each section. Oven-dried sediments were cooled in a desiccator, weighed, placed in a muffle furnace at 500°C for 2 hours, again cooled in a desiccator, and then re-weighed.

Analysis of fossil pigments was carried out on every section from 0 – 15 cm core depth, and every second section from 15 – 75 cm. Samples were freeze-dried, homogenized, and extracted (50–150 mg dry mass) in a mixture of acetone:methanol:water (80:15:5). Extracts were dried completely under a pure N_2 atmosphere, re-dissolved in injection solvent containing Sudan II dye as an internal standard (Sigma Chemical Corporation, Saint Louis, Missouri, USA) (Leavitt and Findlay 1994), and stored at -80°C until analysis by high-performance liquid chromatography (HPLC) following Leavitt and Hodgson (2001).

Carotenoid, chlorophyll, and derivative-compound concentrations were quantified with an Aligent (Hewlett Packard) model 1100 fitted with a 10 cm C18 column (Microsorb, 3 μm particle size). Pigment concentrations were expressed as nanomoles per gram of organic matter (based on LOI measurements described above). Pigment identifications were based on comparisons of chromatographic position, and spectral characteristics were compared with those of authentic standards (Leavitt and Hodgson 2001). Analysis was restricted to chlorophylls *a*, *b*, *a'*, phaeophytins *a* and *b*, and the following carotenoids: alloxanthin (indicator of cryptophytes), diatoxanthin (mainly diatoms), fucoxanthin (silaceous algae and some dinoflagellates), lutein + zeaxanthin (chlorophytes and cyanobacteria), and β-carotene (all algae) (Leavitt and Hodgson 2001).

Preservation of the fossil pigments appeared good, while overall concentrations of individual pigments were extremely low. An abrupt decline in pigment concentrations below 25 cm core depth combined with a change in the physical appearance of the core (discontinuation of varves) suggested that a slump or similar catastrophic event had taken place. Therefore, sediments below 25 cm depth were excluded from any further analyses. A visual inspection of the pigment data suggested that all pigments were highly correlated with each other throughout the upper 25 cm of the core. In order to simplify the analysis the carotenoids were summed to form a single fossil pigments time series, and the more labile chlorophylls and phaeophytins were excluded from the general analysis.

Diatoms

An initial investigation of siliceous diatom fossil concentrations was carried out on 10 subsamples of one of the other 2 cores collected (KI-C2). Permanent Naphrax® mounts of acid cleaned material from each subsample were prepared, a slide was scanned from each level, and a short count of 100 valves (50 cells) was conducted on a slide representing the uppermost section that we subsampled (2.50-2.75 cm).

Data analysis

The high sedimentation rate in Kitlope Lake, combined with the high temporal resolution at which we sectioned the sediment core, resulted in the majority of years sampled being covered by 2-3 core sections. This resulted in an excessive amount of seasonal variation in the N and C data, and to compensate for this variation each section was assigned a median decimal year (*e.g.* 1965.2) based on the modeled ^{210}Pb dates, and all sedimentary data were grouped into one-year bins to allow for direct comparisons between all time series. Due to the aforementioned apparent discontinuity in the core at approximately 25 cm depth, only the top 25 cm (c.1958-2005) could be analyzed for this study. Prior to calculating correlation coefficients between sedimentary and other data, the sedimentary data grouped into one-year bins were further grouped into three-year bins. This helped to compensate for any error in the ^{210}Pb-inferred dates as well as for brood year effects of the sockeye population, so that long term trends in the various time series would be apparent despite the potentially confounding effects of natural inter-cohort variability. Annual data for all time series (i.e. one-year bins for sedimentary data) were smoothed with a three-year running average for graphical representation, with the exception of δ^{13}C which did not appear to exhibit seasonal variation.

Relationships among time series were examined using SPSS v.12 software (SPSS Inc.). Time series were visually and statistically assessed for normality and were generally considered to be normally distributed if the Shapiro-Wilks statistic was not significant at the 0.05 level. Sockeye escapement estimates were not normally distributed and were therefore $\log_{10}$-transformed. Time series were then visually and statistically assessed for temporal autocorrelation at n/4 lags (Box and Jenkins 1970), and serial dependency was considered to be present if the probability of the Box-Ljung statistic was

> 0.05. Total nitrogen (TN), total organic carbon (TOC), organic matter loss-on-ignition (LOI), $\delta^{13}C$, and PDO all exhibited significant autocorrelation. All time series were 1st-difference transformed. TN and TOC values were divided by their corresponding LOI values to reduce the possibility of the confounding effects of early diagenesis (e.g. Hodell and Schelske 1998) and to make them comparable to the fossil pigment concentrations which were expressed as nanomoles per gram organic matter (LOI). This conversion had the added effect of significantly reducing serial correlation in the TN and TOC time series.

Daily mean temperatures from Kemano (air) and the Kitlope Lake outflow (air and water) were 1st-difference transformed to remove temporal autocorrelation and examined for significant cross-correlations at multiple lags. Pearson correlation coefficients were calculated for both raw and 1st-differenced time series of the following variables (in 3-year bins): TN (% N and %N/%LOI), $\delta^{15}N$, TOC (%C and %C/%LOI), $\delta^{13}C$, C/N, LOI, total carotenoids, sockeye escapements, mean annual temperature, mean annual precipitation, and mean annual PDO index values. For these calculations, the most recent 6 years (~ 3 cm) of data were excluded to help ensure that correlations were not skewed by early diagenesis of sediment organic matter. Therefore the final data set for calculation of correlation coefficients consisted of 14 data points. Additional calculations of Pearson coefficients were performed on other time series, including 1st-difference transformed mean annual temperature and PDO values (not grouped into 3-year bins), cross-correlations between PDO, temperature, and sockeye escapements at multiple year lags, as well as alternative treatments of 3-year binned series listed above. Correlation coefficients were not calculated between raw and differenced time series.

Results

Historic abundance and harvest of Kitlope Lake sockeye salmon

The methods and results of the LTEK and archival research are summarized in detail in Appendix A. Briefly, all qualitative accounts from interviews with Haisla elders, combined with cannery pack records and early qualitative observations by fisheries officers (1921-33) consistently suggested or reported that average annual returns of sockeye salmon to Kitlope Lake were substantially higher from year to year from the late 1800s until the late 1940s than they were after about 1950, with the exception of the high returns in the early-mid 1960s. Trends in annual enumerations of sockeye escapement to Kitlope Lake since 1934 were in agreement with the oral record, and estimates ranged from 3500-175 000 (~300-14600 fish km^{-2} lake area) (Figure 2).

Both the LTEK information (Appendix A) and Area 6 Salmon Catch History reports showed that commercial harvest has exerted considerable control over Kitlope Lake sockeye population dynamics. For example, sustained fishing pressure in (gillnet) and near (seine) Gardner Canal in the first half of the 20th century led to declines of multiple stocks which in turn led to a moratorium on fishing in those sub-areas in 1956 that has never been lifted. The sockeye escapements rebounded substantially after the 1956 moratorium (Figure 2). The record high escapement in 1961 followed a brief shift in the PDO from a brief warming phase to a cooling phase (Mantua *et al*. 1997; Figure 5), and there was an unusually long commercial fishers' strike that year that lasted for 3 weeks (July 13 – Aug. 4) during the sockeye migration. Also, the Butedale (Figure 1B–9) cannery was partially shut down for maintenance purposes that year, leaving the boats that remained fishing to dress and ice their own catch, as the next closest cannery (Klemtu) was running at full capacity, thus curtailing fishing efficiency (DFO unpublished Area History Reports).

DFO's Management Target Escapement (MTE) for Kitlope sockeye is 22 000 fish (Shortreed et al. 2001) and is based on the photosynthetic rate model described in Shortreed *et al.* (2000). Despite an abundance of pristine spawning and rearing habitat (Salmonid Rivers Observatory Network, Flathead Lake Biological Station, unpublished data), estimated annual returns of sockeye salmon to Kitlope Lake have averaged

< 10 000 over the last decade, and have not consistently exceeded the MTE since the late 1960s (Figure 2; DFO annual stream escapement reports).

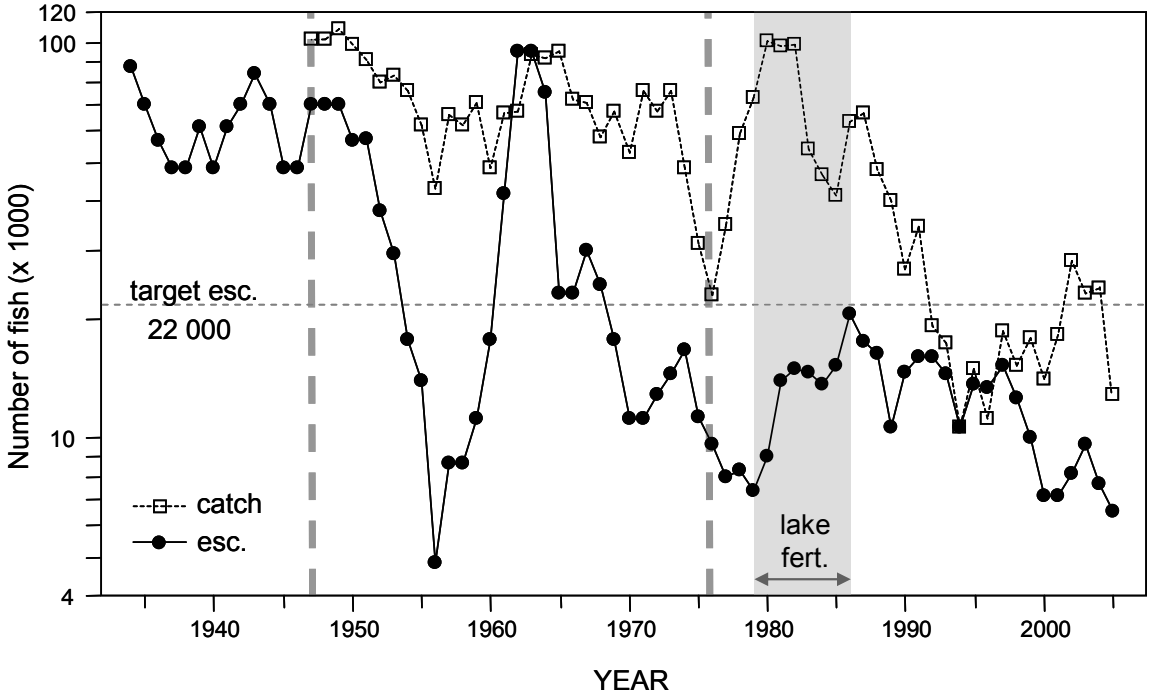

Figure 2. Three-year running averages of estimated numbers of adult sockeye salmon returning to Kitlope Lake (1934-2005) and commercial sockeye catches (all gear types) in DFO statistical Area 6 (1947-2005). Sources: Escapement data from DFO annual stream escapement reports (BC16s – Brian Spilsted, DFO, pers. comm.); catch data from sales slips (Dave Peacock, DFO, pers. comm.). Dashed vertical lines indicate PDO phase shifts (Mantua *et al.* 1997); note logarithmic scale on y-axis.

Climate dynamics

Comparisons among the Kemano daily air temperature data and hourly air and water temperature measurements from temperature loggers placed at the Kitlope Lake outflow showed that LTEK observations from the Kemano area and daily air temperature records from the Kemano weather station (1951-2007) were an excellent proxy for air and surface water temperatures of Kitlope Lake (Figure 3). 1st-difference residuals of Kemano mean daily air temperatures and Kitlope Lake mean daily surface water temperatures were significantly correlated with a 2-day lag ($r = 0.25$, $P < 0.001$, $N = 849$) and all 3 time series were significantly correlated with each other at several lags from 0-2 days over the July 2005 – Oct. 2006 period of data overlap (Figure 4).

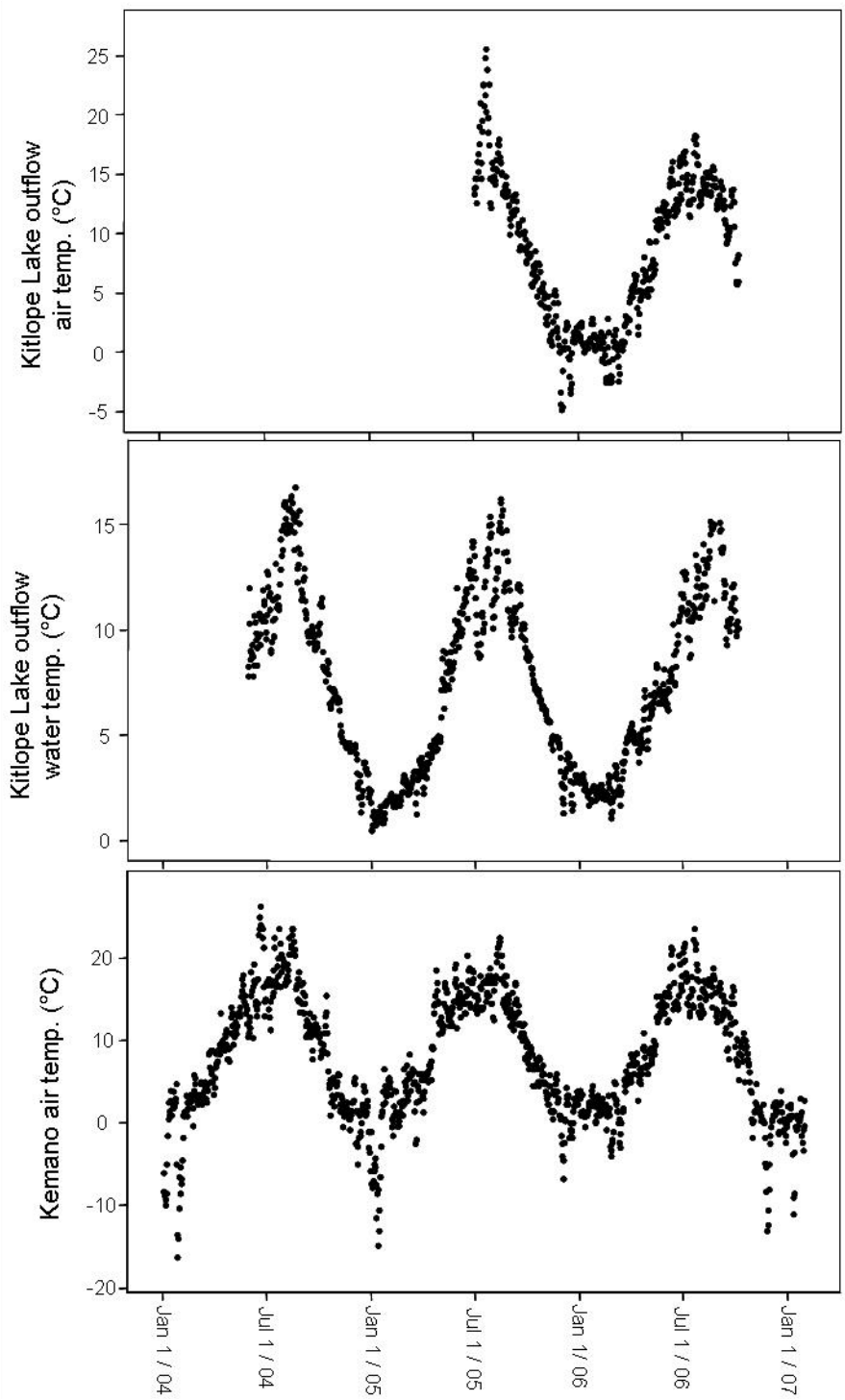

Figure 3. Daily average air temperature from the Kemano weather station (UTM 09U, 570670 m E, 5933986 m N, elev. 87 m; Environment Canada) and daily average water and air temperature measured at the Kitlope Lake outflow (based on hourly measurements from temperature loggers; UTM_{air} 09U, 581793 m E, 5891274m N; UTM_{water} 09U, 582177, 5890940).

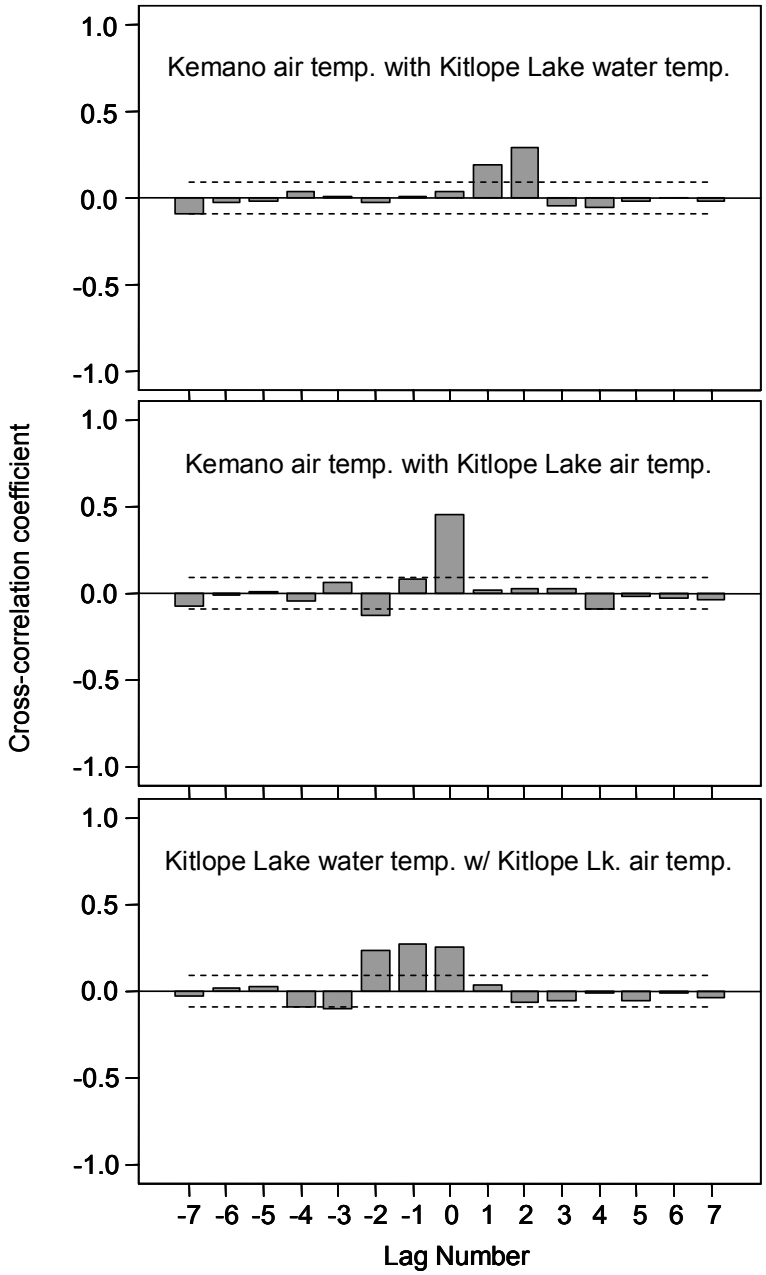

Figure 4. Cross-correlations between 1st-difference residuals of mean daily air temperatures measured at the Kemano weather station and mean daily air and water temperature measured at the Kitlope Lake outflow over the period of data overlap (July 2005 – Oct. 2006; N = 453). Dashed lines denote upper and lower confidence limits (2 standard errors).

Mean annual temperatures in Kemano from 1952 to 2006 ranged from 5.01 to 8.46 °C ($\bar{x}$ = 6.86 ± 0.86 °C std. dev.). While there was considerable variation in temperature over the period of record, there was also a clear warming trend, especially from c.1972-2007 (Figure 5). LTEK gathered from Haisla elders and two local non-Haisla individuals contained strong beliefs that climate warming has decreased the

duration, frequency, and extent of ice-cover in Gardner Canal during the winter months (Appendix A). The sum of the narratives and observations shared by the interviewees and gleaned from previous accounts showed that in the early-mid 20th century the fresh water lens on Gardner Canal tended to freeze over at some point during most winters from the Kitlope estuary past Kemano (Figure 1B), whereas this phenomenon became less and less frequent over the second half of the 20th century, with solid persistent ice not forming in several decades, and solid ephemeral ice not forming in the past 6 years (Appendix A).

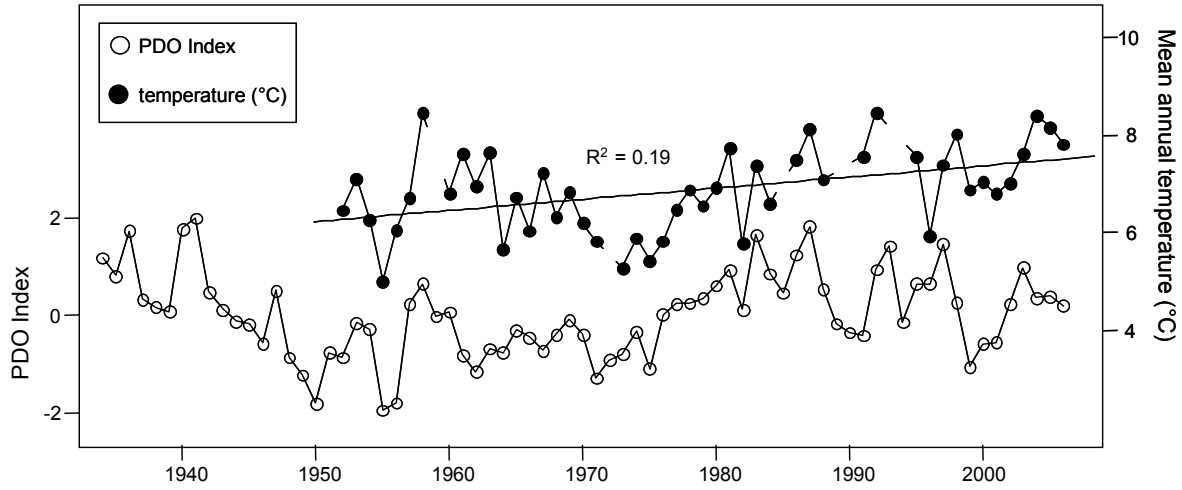

Figure 5. Mean annual air temperature from 1952 to 2006 based on daily readings at Kemano, BC (UTM 09U, 570670 m E, 5933986m N, elevation 87 m), approximately 46 km from Kitlope Lake (Souce: Environment Canada); and mean annual Pacific Decadal Oscillation (PDO) index values (Source: University of Washington Joint Institute for the Atmosphere and Oceans). First-difference residuals of the two variables are significantly correlated (r = 0.48, P < 0.001, missing temp. values interpolated).

The PDO index 1st-difference residuals were correlated with mean annual air temperature residuals at lag 0 (1952-2006 with missing temp. values interpolated; r = 0.48, P < 0.001; Figure 5) and correlations at all other lags were not significant. Cross-correlations between residuals for sockeye escapements and temperature (1952-2005) were significant at lag 0 (r = 0.28, P < 0.05) and lag -5 (r = 0.39, P < 0.01), and no others, and no cross-correlations were significant between PDO and sockeye escapements. Mean annual precipitation was not significantly correlated with PDO, temperature, or sockeye escapements, nor was it correlated with any of the sedimentary proxies (Table 3).

Taken together, the quantitative and qualitative climatic data sets strongly suggested that the annual ice-free period on Kitlope Lake increased over the lifetimes of the interviewees (approx. 60 – 75 years) along with average air temperatures, and these changes were coherent with basin-wide ocean-atmosphere climatic regimes.

Sediment chronology

We documented an approximate exponential decrease in ^{210}Pb activity as a function of depth in core KI-C1 (Figure 6) showing that the core could be aged accurately. Indeed, the surface total activity was ~15 times the lowest ^{210}Pb level of ~0.80 disintegrations per minute (DPM) g^{-1} at 65.5-65.75 cm depth, and ^{226}Ra was measured at 0.86, 0.92 and 2.28 DPM g^{-1} in the depths of 55.5 - 55.75 cm, 65.5 - 65.75 cm, and 75.25 - 75.5 cm, respectively, likely confirming that the lowest ^{210}Pb activity was the background level. The ^{210}Pb activity increased to about 3.22 DPM g^{-1} in the deepest section and it is believed that this was due to increased ^{226}Ra in this section.

An obvious discontinuity occurred in the core at about 25 cm depth: semi-sequential varving was visible above but not below 25 cm depth and fossil pigment concentrations declined steeply below this depth. A slump with subsequent sediment mixing was the most likely explanation for the observed changes. However, the sedimentary unconformity was not indicated by the ^{210}Pb decay curve (Figure 6). This may have been a coincidental result of the sample depths of systematically selected sections for ^{210}Pb analysis in relation to the unconformity. Nevertheless, the ^{210}Pb and ^{226}Ra data showed that background ^{210}Pb levels were likely reached, thus satisfying the basic premise of the constant-rate-of-supply (CRS) model used to date this core. That is, the age of sediments at a given core depth can be calculated by comparing the cumulative excess ^{210}Po activity (DPM cm^{-2}) of sediments below that depth with the total excess ^{210}Po in the core (Appleby and Oldfield 1978). As such, we concluded that the modeled dates for the core above the unconformity were accurate. Moreover, the conservative numerical approach we used to test relationships between sedimentary and other time series (i.e. grouping data into 3-year bins) ensured that our calculations of Pearson correlation coefficients would likely be robust to dating error. Strong consistency

between some sedimentary – non-sedimentary time series pairs (e.g. $\delta^{15}N$ – air temperature; see below) provided further indication that our date estimates were accurate.

Based on the CRS model, the portion of the core unaffected by the apparent slump (0 – 25.0 cm) covered approx. 48 years, yielding an average sediment accumulation rate in the upper 25 cm of the core (c.1957-2005) of approx. 4.7 mm $year^{-1}$. The extremely high sedimentation rate confirms the high prevalence of glacial silt in Kitlope Lake measured by others (Stockner *et al*. 1993).

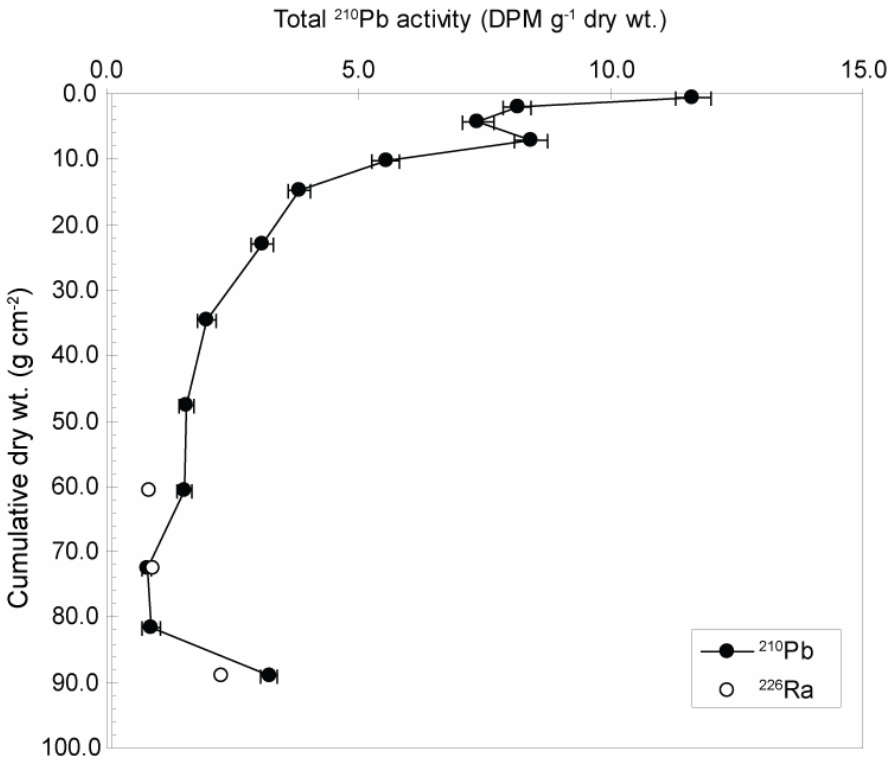

Figure 6. Depth profile of ^{210}Pb activity measurements for Kitlope Lake sediment core C1. The three ^{226}Ra measurements confirm that the increased ^{210}Pb activity in the deepest measurement is likely due to increased ^{226}Ra.

Carbon and nitrogen storage and isotope ratios in Kitlope Lake sediments

Average values for total N and organic C (TN and TOC; Table 2) were extremely low in Kitlope Lake sediments, but fluctuated throughout the upper 25 cm of the core, and generally decreased with depth. Sedimentary $\delta^{15}N$ and organic C/N exhibited substantial fluctuations through the core (± 2.07 ‰ and ± 3.55, respectively), which along with the TN and TOC fluctuations, indicated that substantial changes in organic

matter source occurred over the period covered by the core (Table 2; Figure 9). The high organic mass C/N ratio ($\bar{x}$ = 16.77 ± 1.44 std.dev.) indicated that a substantial but not overwhelming portion of the sedimentary organic matter was likely of terrestrial origin (Meyers and Teranes 2001). TN, TOC, and $\delta^{15}N$ all increased sharply in the most recent ~5 years.

Sedimentary $\delta^{13}C$ also fluctuated, although to a much lesser extent than the above variables, and generally increased with depth (Figure 9). Seasonal variations (i.e. between adjacent core sections – not shown) were not discernable in the sedimentary $\delta^{13}C$, demonstrating that it is robust to seasonal changes in organic matter concentration (LOI, see below), as well as to changes in C/N and $\delta^{15}N$, all of which did exhibit substantial seasonal variations (note that $\delta^{13}C$ is the only sedimentary time series shown in Figure 9 that is not smoothed with a running average).

The relationship between %N and %C was linear with a negative %N intercept (%N = 0.07(%C) - 0.016; Figure 7), thus demonstrating that concentrations of inorganically-bound nitrogen were negligible, as nitrogen was not present in excess of that associated with organic matter (i.e. carbon). We therefore inferred that measured $\delta^{15}N$ values were generally indicative of the isotopic composition of sediment organic matter rather than clay-adsorbed ammonium (Talbot 2001).

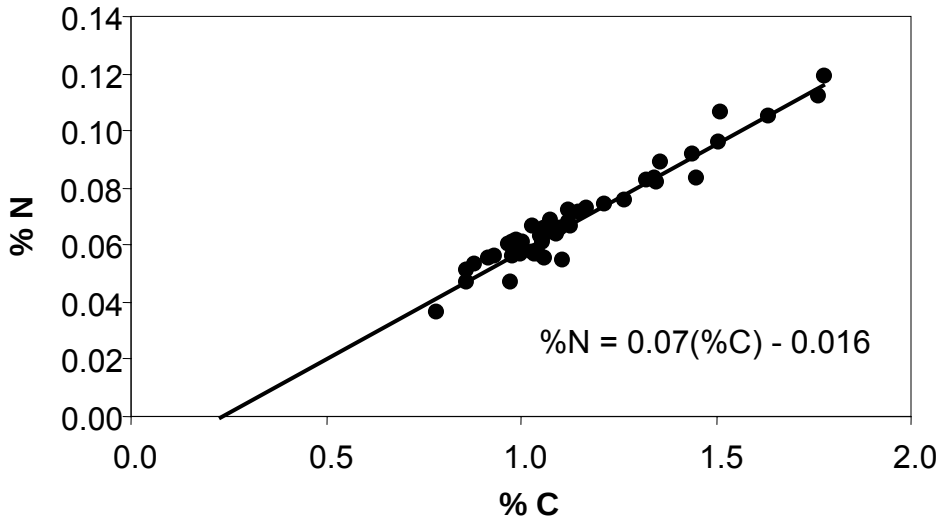

Figure 7. Linear relationship between total nitrogen and carbon (% mass) for all samples obtained from core KI-C1 (r = 0.89, P < 0.001 for 1st-difference residuals).

Recall that we excluded data for the most recent 6 years (upper ~3 cm) (see *Methods – Data analysis* for rationale) for determination of correlations between time series variables. First-differenced sediment organic matter concentrations from 1958 – 1999 were significantly correlated with total carbon ($r = 0.79$, $P = 0.001$) and total nitrogen ($r = 0.73$, $P = 0.002$), and 1st-difference residuals of C and N were significantly correlated with each other ($r = 0.89$, $P < 0.001$, raw values shown in Figure 7), thus providing further indication that the bulk of sedimentary C and N was associated with organic matter. Organic C/N was negatively correlated with LOI-corrected TN ($r = -0.78$, $P = 0.001$) but not with LOI-corrected TOC ($r = -0.28$, $P = 0.33$) (Table 3), implying that although TOC and TN both decreased with depth (Figure 9), the increase in the C/N ratio with depth was a result of a proportionately greater decrease in total N. Further, the strong negative correlation between $\delta^{15}N$ and C/N (raw: $r = -0.50$, $P = 0.07$; differenced: $r = -0.85$, $P < 0.001$) shows that when the organic C/N ratio was lower due to an increased sedimentary N concentration, the N was also isotopically enriched.

The highest $\delta^{15}N$ values in the core coincided with the highest sockeye escapements on record, with an offset of approximately 1.5 years that could easily be attributable to dating error (Figure 9) but, due to the 3-year bins we used, the correlation coefficients should not have been affected by this offset. $\delta^{15}N$ tracked sockeye escapements closely from 1958-1975 ($r = 0.89$, $P = 0.02$ for 1st-difference residuals) but the association between the two variables was more tenuous after that. Sedimentary $\delta^{15}N$ was not significantly correlated with sockeye escapements from 1958-1999 ($r = 0.39$, $P = 0.17$) unless a 5-point running average was applied to the raw $\delta^{15}N$ time series prior to consolidation into 3-year bins ($r = 0.59$, $P < 0.03$). $\delta^{15}N$ was significantly correlated with mean annual air temperature ($r = 0.57$, $P = 0.34$), and the two variables appear to track closely throughout the core (Figure 9). The organic C/N ratio inversely tracked $\delta^{15}N$ in the lower and upper portions of the core, and to a lesser extent through the rest of the core (Figure 9). The inclusion of the upper sections in the analysis increased both the strength and significance of the negative correlation (upper layers excluded: $r = -0.50$, $P = 0.07$; whole core: $r = -0.57$, $P = 0.02$). Differenced, but not raw, C/N and sockeye time series were negatively correlated ($r = -0.53$, $P < 0.1$; Table 3). On the whole these results show that in addition to sockeye-derived MDN, other factors have likely influenced the

isotopic composition of sedimentary N, with climate being of particular importance, especially after about 1975 (Figure 9).

Table 2. Minimum, maximum, and mean values with standard deviations for various analyses of all samples obtained from core KI-C1; these data summarize the period 1956-2005.

	Minimum	Maximum	Mean	Std. deviation
Total nitrogen (%)	0.04	0.12	0.07	0.02
$\delta^{15}N$ (‰)	-2.61	1.53	-0.33	0.82
Total carbon (%)	0.78	1.86	1.16	0.25
$\delta^{13}C$ (‰)	-27.74	-25.88	-26.71	0.37
C/N (by weight)	14.25	21.35	16.77	1.44
Organic matter (%)	2.90	5.35	3.75	0.56
Carotenoids (nmol g^{-1} org. matter)	2.80	23.48	8.61	3.52

Fossil pigments and sediment organic matter

Sediment organic matter content was very low, between 2.9 – 5.4 % (mean 3.75 ± 0.56 %; Table 2), as expected given the lake's low primary and secondary productivity and high inputs of glacial sediment from the Tezwa drainage (Table 1; Stockner *et al*. 1993). Organic matter concentrations were generally stable over the past 48 years with two exceptions: a spike from about 1987-1989, and a steady increase in the most recent 5 years, both of which were apparent in the TN and TOC curves (Figure 9). The spike c.1987-1989 was likely due to residual terrestrial organic matter, as small terrestrial macrofossils were removed from these sections (9.5-10.5 cm depth) during sieving and a flood of record is known to have occurred in September 1988.

Concentrations of organic-matter-specific sedimentary fossil carotenoids were very low and fluctuated substantially over the past 48 years ($\bar{x}$ = 8.61 nmol g^{-1} org. ± 3.52 std.dev.). In general, they increased over time reaching their highest concentrations c.2003, and appear to have declined during most of the 6-year fertilization period (Figure 9). Ratios of chlorophyll-*a* to phaeophytin-*a* were low and, with the exception of the upper 1.5 cm (~ 3.5 years), were relatively stable over the top 25 cm of the core (range 0.25 – 0.54; mean 0.38 ± 0.05 std. dev.; Figure 8), suggesting substantial pre-burial

degradation followed by good post-burial preservation. The excursions in the chlorophyll-*a* to phaeophytin-*a* ratio in the most recent ~ 3.5 years suggested that fossil carotenoids for those sections may not be comparable to those from the rest of the core.

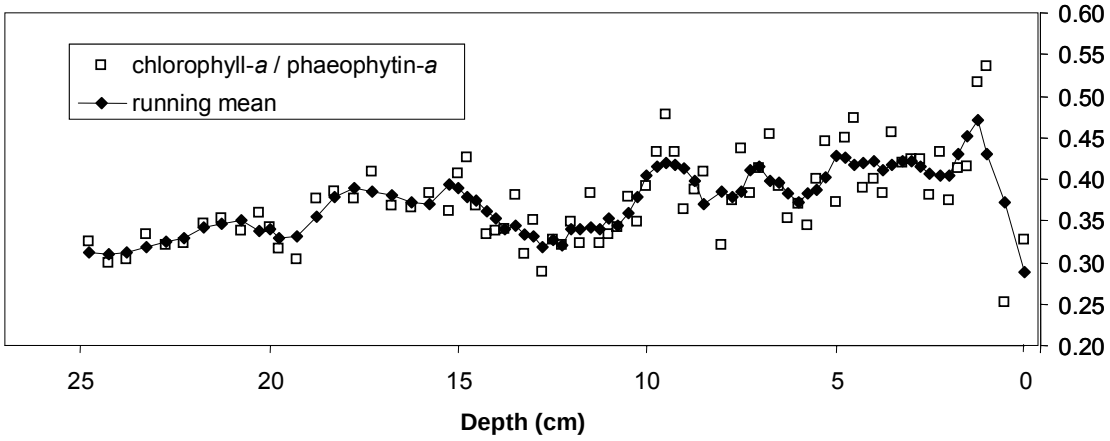

Figure 8. Downcore ratio of chlorophyll-*a* to phaeophytin-*a* in Kitlope Lake core C1.

Fossil carotenoids were highly correlated with LOI-corrected TN ($r = 0.70$, $P = 0.005$) and LOI-corrected TOC ($r = 0.79$, $P = 0.001$; Table 3), suggesting (along with above correlations among LOI, TN, and TOC) that sedimentary organic matter was largely derived from detrital materials containing photosynthetic pigments. 1st-difference residuals of fossil carotenoids and $\delta^{13}C$ were negatively correlated ($r = -0.66$, $P < 0.01$; Table 3), which due to the relative stability of $\delta^{13}C$ over time (Hodell and Schelske 1998), confirmed that trends in the more labile compounds (i.e. carotenoids, TN, TOC) were likely of ecologically significance.

Fossil carotenoids were not correlated with sockeye escapements ($r = -0.22$, $P = 0.45$), but the highest carotenoid concentrations from c.1960-1970 coincided with the 1963 record high sockeye escapement (Figure 9), implying that at lower spawner densities salmon-derived MDN does not significantly influence aquatic primary productivity in Kitlope Lake. Although TN and TOC were correlated with both C/N and fossil pigments, organic C/N was negatively correlated with organic-matter-specific fossil carotenoids only if the upper layers were included ($r = -0.55$, $P = 0.03$), providing further evidence that dominant inputs of organic matter to the lake sediments have likely fluctuated between algal and terrestrial sources over the past 48 years.

Diatoms

We determined that diatoms were too sparse at all core depths for counts. Moreover, the utility of diatom analyses as indicators of lake water quality would have been questionable as periphytic forms were predominant in all 10 subsamples. The uppermost level (2.50-2.75 cm) described below was generally representative of the other 9 subsamples. *Tabellaria* sp. was the only true planktonic diatom present and it represented only 2% of the diatom assemblage. We did not find any centrics (*e.g.*, *Cyclotella, Stephanodiscus*) and the remaining taxa were benthic forms. Among them were 8 species of *Eunotia*, a genus that is associated with the epiphyton and metaphyton of oligotrophic waters (Round *et al.* 1990). The Tezwa River watershed was determined to be the most likely source of these periphytic forms.

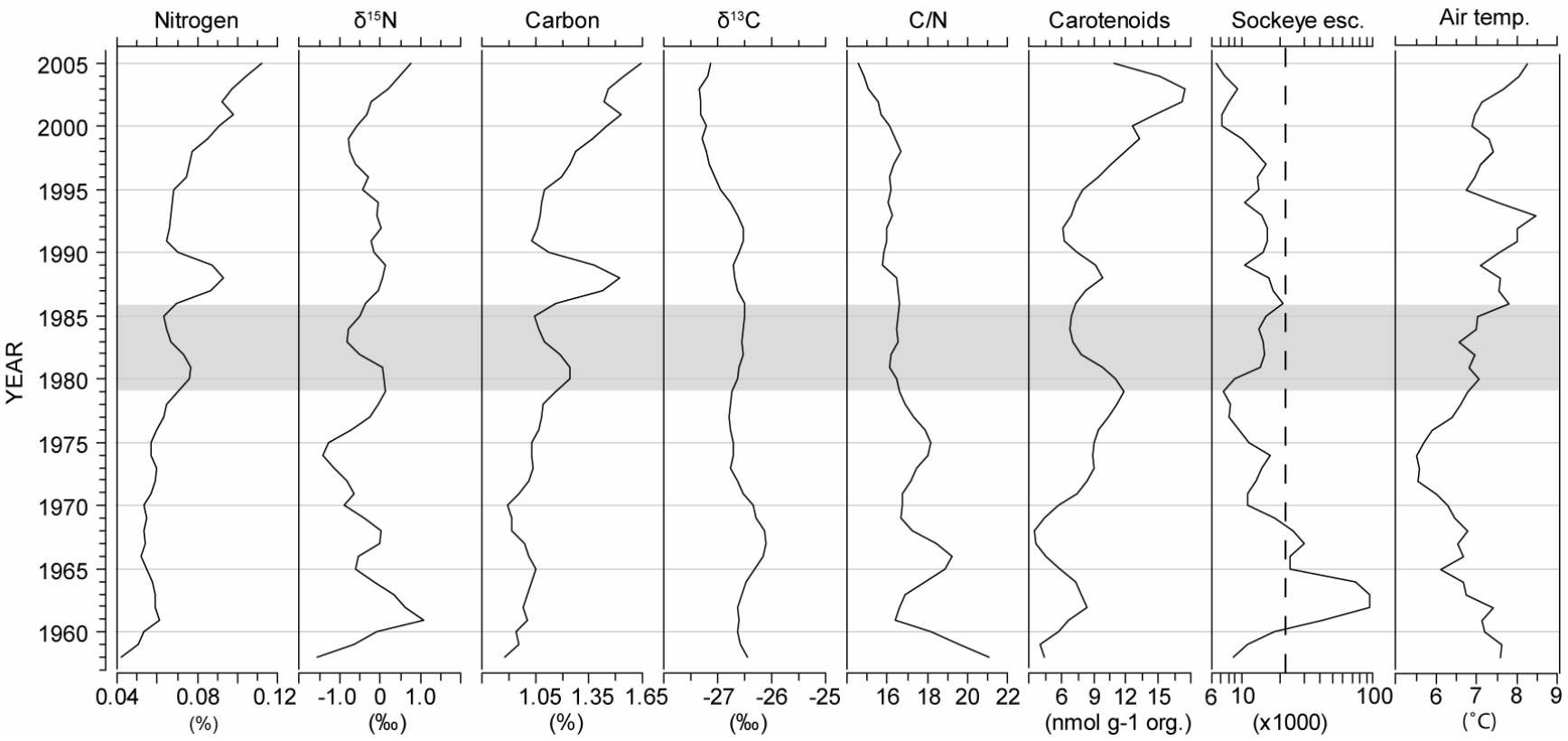

Figure 9. Comparison of ^{210}Pb-dated sedimentary time series from Kitlope Lake with sockeye salmon escapement estimates (note logarithmic scale) and mean air temperatures. All time series except δ^{13}C were smoothed with a 3-year running average. C/N is the ratio of organic carbon to nitrogen by weight. Carotenoids are the sum total nanomoles of alloxanthin, diatoxanthin, fucoxanthin, lutein + zeaxanthin, and β-carotene per gram of organic matter. The grey shading marks the period of artificial fertilization and the vertical dashed line marks the management target sockeye escapement of 22 000 fish.

Table 3. Pearson correlation matrix for sedimentary, climate, and sockeye escapement time series data (raw and 1st-differenced) for samples describing the period 1958-1999. Italicized coefficients indicate the presence of significant temporal autocorrelation in at least one of the two time series. Sockeye escapements were log_{10}-transformed to normalize data distribution. Raw (but not differenced) TN and TOC values were divided by % organic matter to reduce serial correlation and facilitate comparison with organic-matter-specific carotenoid concentrations.

raw time series

P < 0.01 P < 0.05 P < 0.10	TN (%)	$\delta^{15}N$	$\delta^{15}N$ smooth	TOC (%)	$\delta^{13}C$	C/N ratio	LOI (%)	Carot-enoids	sock. esc.	temp.	precip.	PDO
TN (%)		.23	.31	.80	*-.44*	-.78	*.29*	.70	-.09	.05	*.04*	*.22*
$\delta^{15}N$	.39		.92	-.07	*.18*	-.50	*.07*	-.09	.39	.57	*.16*	*.02*
$\delta^{15}N$ smooth	.47	.92		.10	*.23*	-.43	*-.02*	-.02	.59	.47	*.19*	*-.06*
TOC (%)	.89	.04	.13		*-.28*	-.28	*.02*	.79	-.08	-.28	*.14*	*-.02*
$\delta^{13}C$	-.40	.02	.02	-.38		*.30*	*-.48*	*-.70*	*.31*	*-.07*	*.01*	*-.15*
C/N ratio	-.39	-.85	-.84	.05	.13		*-.34*	-.29	.02	-.28	*.13*	*-.31*
LOI (%)	.73	-.03	-.11	.79	-.37	.07		*.29*	*-.45*	*.52*	*.18*	*.62*
Carotenoids	.68	.08	.22	.74	-.66	-.09	.38		-.22	-.16	*-.01*	*.05*
sock. esc.	-.11	.40	.56	-.34	.05	-.53	-.61	-.02		.16	*.24*	*-.40*
temp.	-.09	.54	.37	-.21	.33	-.23	-.13	-.26	.28		*.37*	*.57*
precip.	-.13	-.06	-.12	.09	.16	.37	-.06	.05	.06	.36		*-.11*
PDO	-.56	-.20	-.35	-.39	.53	.45	-.15	-.53	-.22	.49	.20	

1st-difference residuals

Discussion

Controls on sockeye dynamics and habitat: climate and harvest

In the absence of substantial habitat alterations and complications arising from hatchery supplementation (e.g. Waples 1991), climate and harvest are key drivers of Pacific salmon populations (e.g. Finney *et al.* 2000). A substantial decreasing trend in sockeye escapements to Kitlope Lake over the past century was demonstrated through government escapement estimates and local and traditional ecological knowledge (LTEK; Appendix A). Similar stock declines have occurred in most other systems on the north and central coasts of BC (Harvey and MacDuffee 2002), and Kitlope sockeye are certainly not noteworthy in this regard. However, the abundance of excellent spawning habitat (Rosberg *et al*. 1982; SaRON unpublished data) and perpetual absence of anthropogenic disturbance and hatchery-related impacts within the watershed[1] allow us to narrow our focus when considering the causes of these declines in the Kitlope.

Mean annual air temperatures from the Kemano weather station were significantly and positively correlated with mean annual Pacific Decadal Oscillation (PDO) values demonstrating that the PDO is a reliable indicator of general climatic conditions in the region, and that regional climatic trends are significantly tied to basin-wide ocean-atmosphere climatic trends. The fact that several of the sedimentary proxies were correlated with either PDO or temperature, but not both, reminds us that while temperature and PDO are strongly correlated they are measures of overlapping but ultimately different parameters.

The lack of correlation between mean annual precipitation and any other variable in our analysis was quite surprising given the strong influence that hydrology exerts on aquatic primary productivity and delivery of terrestrial materials to Kitlope Lake (Stockner *et al*. 1993). The most likely explanation for this apparent disconnect is that mean annual precipitation (rain + snow) is too crude of a measure, and some other metric of precipitation and/or associated stream discharge may better reflect the hydrologic

[1] The nearest hatchery is on the Kitimat River, ~ 140 km (by water) from the Kitlope Estuary, and hatches coho (*Oncorhynchus kisutch*), chinook (*O. Tshawytscha*), chum (*O. keta*), cutthroat (*O. clarkii*), and steelhead (*O. mykiss*), but not sockeye.

processes that control aquatic primary production and delivery of terrestrial N and organic matter to Kitlope Lake.

Mean annual air temperature was significantly and positively correlated with sockeye escapements from 1951 – 2005 only at the -5 lag and 0 lag, and the majority of Kitlope sockeye are on a 5_2 life cycle with 4_2 being nearly as common (Rosberg *et al*. 1982), indicating that climate may have exerted considerable control over the Kitlope sockeye population. Moreover, this indicated that there was likely a significant brood-year (i.e. lag -5) effect despite the confounding effects of the commercial fishery. The brood-year effect could be a reflection of climatic effects on migrating adults both before and after entering fresh water, or it could be a reflection of climate-related factors affecting spawning success and egg survival, or any combination of these and other factors. The significant positive correlation at lag 0 may reflect an effect of temperature-mediated ocean productivity on sockeye survival during the spawning migration. Without substantiating fry survival and/or smolt outmigration data, stock composition data for the commercial catch, and more sophisticated analysis than we provide here, we can only speculate as to the extent that climatic factors were more critically limiting at one location or life history stage or another. Moreover, the potential for error in the escapement estimates ultimately prevents us from making definitive conclusions based on estimates from individual years, as opposed to averages across multiple years.

We found no significant correlation between either the 1^{st}-differenced or raw PDO and sockeye escapement time series at any lag between -5 and 5. However, strong relationships between sockeye population dynamics and large-scale climate regimes have been demonstrated in many systems to the north (southwest Alaska) and south (Fraser and Columbia) of the Kitlope (Beamish *et al.* 1997; Mantua *et al.* 1997; Finney *et al.* 2000) and we found that local air temperatures were significantly correlated with escapements at 2 ecologically meaningful lags. This discrepancy suggests that, while the local climate was closely regulated by ocean atmosphere climate regimes, survival rates for Kitlope Lake sockeye were more closely associated with climatic conditions at the regional scale (*e.g.* Gardner Canal and its coastal approach waters) than at the scale of the North Pacific Ocean. This interpretation is supported by a study that demonstrated stronger coherence in production within regions than among regions for B.C. and Alaska

sockeye stocks (Peterman *et al.* 1998), and another study showing that environmental processes exert more control on sockeye survival at local and regional (< 500 km) scales, than at oceanic scales (Pyper *et al.* 2005).

Historic and recent impacts of the area 6 commercial catch on Kitlope sockeye spawning populations and subsequent recruitment were difficult to quantify. The mixed-stock fishery has largely been conducted in the coastal approach waters to Douglas Channel, over 120 km by water from the mouth of the Kitlope River, and has tended to target chum and pink salmon produced at the Kitimat River hatchery since large-scale production began there in 1983. The stock composition of the sockeye catch is generally unknown (Dave Peacock, DFO, pers.comm.) exacerbating otherwise surmountable uncertainties presented by changes in fishing fleet behaviour over time. This is a common problem in most mixed-stock fisheries on the BC coast, and is not unique to Kitlope River and other Area 6 stocks.

Despite the paucity of stock composition information for the commercial fishery, we were able to qualitatively assess the relationship between fishing pressure and escapement of sockeye to Kitlope Lake over approximately the past century using a combination of LTEK and DFO Area History of Salmon Catch reports (1947-1983). It is clear from salmon cannery pack records and LTEK that Kitlope sockeye supported substantial subsistence fisheries for large pre-smallpox communities of Henaaksiala and Haisla people, and substantial commercial fisheries over the past 120 years. Not surprisingly, historical information collected from various sources also indicated that continued fishing pressure exerted strong controls on Kitlope sockeye escapements over the years. This suggested that high harvest levels were at least partly responsible for reduced catches and escapement over the past two decades or so, in which sockeye escapements consistently did not meet their target escapement. While the lack of accurate catch composition data precluded an accurate quantification of the relative controls that climate and harvest exert on Kitlope sockeye returns, our interpretation of the available information was that both factors were important to some degree.

Another problem presented by the lack of reliable catch estimates for Kitlope sockeye relates to the lake fertilization program (1979-83, 1985). The average mass of sockeye fry in the lake increased from 2.1g in the year prior to the beginning of the

fertilization program, to 5.2 g in the following two fertilized years (Hyatt and Stockner 1985) and sockeye escapements apparently increased in subsequent brood years (Figure 2). However, the best metric of success for the fertilization program would be the number of recruits per spawner and/or smolt in fertilized vs. unfertilized years which, in the absence of smolt outmigration and stock-specific commercial catch estimates, is impossible to calculate.

Interpretation of productivity proxies in lake sediments

General overview and comparisons with other sockeye nursery lakes

The 1958-2005 sedimentary record in Kitlope Lake was characterized by low total nitrogen (TN) and organic carbon (TOC), and low organic-specific fossil carotenoid concentrations, confirming Kitlope Lake's position on the bottom of the trophic spectrum of sockeye nursery lakes in British Columbia (Shortreed *et al.* 2001). Total sedimentary nitrogen and organic carbon concentrations are rarely reported in other paleolimnological studies of sockeye nursery lakes, but the concentrations we found in Kitlope Lake were extremely low compared to other literature values (e.g. Hu *et al.* 2001; Talbot 2001). This was most likely a combined effect of extremely high sediment loading dominated by glacial flour from the watershed combined with the extremely low trophic status of the system (Stockner *et al.* 1993). The fact that both variables were strongly correlated with sediment organic matter (LOI), as well as with each other, supported our previous conclusions that concentrations of inorganic forms of both elements in the sediments were negligible. Sedimentary mass C/N ratios (14.25 – 21.35 overall and 15.34 for the upper 2 cm) were within the normal range compared to other sockeye nursery lakes in British Columbia (7.9 - 23.3; Brahney *et al.* 2006) and other large temperate oligotrophic lakes worldwide (Meyers and Teranes 2001).

The mean sedimentary $\delta^{15}N$ values we found in Kitlope Lake (-0.33 ‰ for the 25 cm core and 0.09 ‰ for surface sediments (upper 2 cm)) appear to be the lowest yet reported for a sockeye salmon nursery lake (Finney *et al.* 2000; Barto 2004; Gregory-Eaves *et al.* 2004; Holtham *et al.* 2004; Schindler *et al.* 2005a; Brahney *et al.* 2006; Schindler *et al.* 2006; Brock *et al.* in press) and are low even compared to non-sockeye

reference lakes used in those same studies. The sedimentary $\delta^{13}C$ record of Kitlope Lake is discussed below.

The extremely low concentrations of fossil carotenoids, as with total N and organic C, were attributed to high sediment loading from the watershed, and extreme nutrient limitation resulting in a small phytoplankton standing crop (Stockner *et al.* 1993). The significant correlations between TN, TOC, and fossil carotenoids supported each others' validity as measures of changes in the lake's trophic status over time. A comparison of fossil pigment concentrations among sockeye nursery lakes would not be particularly meaningful as various pigments are analyzed in a variety of ways among different lakes. For example, we report only total carotenoid concentrations here, and we do so using units of nmol g^{-1} organic matter (based on our LOI measurements) – a common practice, the justification for which is explained below. However, many others report fossil pigment concentrations in units of nmol g^{-1} total sediment dry weight.

Our diatom findings agreed with analyses of mid-lake epilimnetic phytoplankton assemblages conducted by Stockner *et al*. (1993). They found that diatoms were very few relative to the other plankton taxa present, and that except for *Cyclotella* spp., most of the diatoms they found were associated with periphytic habitats. We did not find any *Cyclotella* spp. in the sediments. However, we agree with Stockner *et al*. (1993) that the most likely source of the benthic forms was the Tezwa River, as Kitlope Lake does not have a well-defined littoral zone in any area of the lake that could have delivered substantial numbers of diatoms to a mid-lake core or epilimnetic sampling location.

Nutrients and productivity in relation to salmon escapements to Kitlope Lake

Strong coherence among $\delta^{15}N$, fossil carotenoids, and sockeye escapements were apparent in the core up until the mid 1970s but after that the relationships were more tenuous. In sockeye nursery lakes that are not N-limited but rather P-limited (or co-limited), such as Kitlope Lake (Stockner *et al*. 1993; Table 1), we can expect an approximately linear relationship between sockeye escapements and sedimentary $\delta^{15}N$ (Brahney *et al.* 2006). Our results show that the order-of-magnitude fluctuations in sockeye escapements from c.1958-1975 likely had a significant effect on the trophic

status of Kitlope Lake, despite its high flushing rate and significant terrestrial inputs as shown by the organic C/N ratio ($\bar{x}$ = 16.77 ± 1.44 std.dev.).

These findings were somewhat different than those of Holtham *et al*. (2004), who found that sockeye nursery lakes with high flushing rates and substantial terrestrial inputs were not strongly influenced by MDN flux. This discrepancy could be explained by the fact that the lakes in their study drained much smaller watersheds (41 – 90 km^2) and had much smaller lake/catchment area ratios (~ 0.03 – 0.09) than Kitlope Lake (872 km^2 and ~ 0.01, respectively). The majority of Kitlope Lake sockeye spawn in the Tezwa River and Kalitan Creek, as much as 20 km upstream of Kitlope Lake (Rosberg *et al.* 1982; Stan Hutchins, DFO, pers.comm.). Fall floods are frequent in the Kitlope watershed (Figure 10c) and so a substantial proportion of spawned-out carcasses are likely to be flushed downstream to decompose in Kitlope Lake (Gende *et al.* 2004). However, a similar proportion of the sockeye biomass is likely retained and cycled upstream through predation (Reimchen 2000; Helfield and Naiman 2006) and entrainment in woody debris (Cederholm *et al.* 1989). The bulk of the MDN from the retained carcasses would then be cycled downstream through the riparian, rheic, and hyporheic foodwebs over time scales that range from days to months (O'Keefe and Edwards 2003). The extremely high daily flushing rate of Kitlope Lake's surface layer suggests that if MDN were to be bioavailable for limnetic primary production in ecologically significant concentrations, most of the cycling would have to take place upstream of the lake. Salmon-derived MDN have been shown to significantly increase autochthonous production in streams in BC (Johnston *et al.* 2004) and Alaska (Chaloner *et al.* 2007). Therefore the predominance of periphytic diatoms over planktonic species in both water (Stockner *et al*. 1993) and sediment samples from Kitlope Lake supports the notion that upstream autochthonous production was an important factor in the sedimentary legacy of salmon abundance and the trophic status of Kitlope Lake.

Fossil carotenoid concentrations appeared to steadily decline during the first 5 out of the 6 years that the lake was artificially fertilized (1979-83, 1985; Figure 9). This observation appears to further underscore the importance of upstream nutrient cycling in this fast-flushing but expansive watershed. Nutrient additions to the lake's fast-flushing surface layer would have been rapidly flushed compared to slowly-cycled nutrients from

salmon carcasses and terrestrial sources in the tributary. Furthermore, the doubling of chlorophyll and zooplankton concentrations after the first year of fertilization (Stockner *et al*. 1993; Table 1) may have been related to a longer-term increase in algal production that appeared to begin in the late 1960s according to the sedimentary fossil carotenoid data (Figure 9). Limnological surveys were only conducted during the first two years of the fertilization program, so we do not know if the apparent decline in algal production during the fertilization program inferred from fossil carotenoids was reflected in limnetic chlorophyll and zooplankton concentrations.

Organic matter source, nutrient limitation, and diagenesis

Organic C/N ratios are widely used in paleolimnology to indicate the relative contributions of autochthonous (aquatic) and allochthonous (terrestrial) production to bulk sediments. Terrestrial primary producers, especially cellulose-rich vascular plants, have much higher organic C/N (> ~20) than do protein-rich lake algae (< ~10) (Meyers and Teranes 2001). The average sedimentary C/N in Kitlope Lake therefore indicates similar historical contributions of both terrestrial and aquatic organic matter, with the general decline over time indicating an increasing algal contribution. Organic C/N was negatively correlated with total N, $\delta^{15}N$, and sockeye escapements, especially in the lower portion of the core. We generally interpret this result as an indication of the influence that sockeye-derived MDN had on lake trophic status up until about 1975.

Brahney *et al*. (2006) hypothesized that in large sockeye nursery lakes terrestrial contributions to sediment organic matter are likely to be insignificant compared to aquatic contributions, and that sedimentary C/N ratios are more likely to reflect changes in the availability of dissolved organic nitrogen to lake algae. We agree with the conclusions in their study, and concur that they are likely applicable to larger N-limited sockeye nursery lakes in British Columbia where terrestrial inputs are negligible. However, we doubt that they apply here as Kitlope Lake is likely P-limited based on molar N:P ratios derived from the water chemistry data summarized in Table 1 ($N:P_{total}$ = 43; $N:P_{dissolved}$ = 53; n = 4). Furthermore, Kitlope Lake has a high catchment to lake area ratio; the complex alluvial floodplains of Kalitan Creek and the upper Tezwa River provide extensive but frequently-flushed off-channel habitats where leaf litter dominated

by N-rich red alder leaves accumulates (Figure 10a,b); frequent and flashy flooding of these tributaries moves substantial amounts of terrestrial debris into the lake (Figure 10c); and terrestrial macrofossils were extracted from sediment samples during sieving prior to C and N analyses.

Figure 10. Representative photographs of: (A) riparian red alder (*Alnus rubra*) pole stand characteristic of the Tezwa River floodplain upstream from Kitlope Lake; (B) Kitlope watershed springbrook habitat in flood channels with alder-dominated canopy (note abundant leaf litter); (C) large trees in transport during bankfull flows in the lower Kitlope River.

Caution must be used when interpreting the ecological significance of the paleoecological trends in the more recent sediments due to the confounding effects of early diagenesis of sediment organic matter. In sediments heavily influenced by terrestrial organic matter the organic C/N ratio will likely decrease over time with the degradation of carbon-rich compounds (Meyers *et al.* 1995), while the C/N of algae-dominated sediments will likely increase over time with the degradation of labile N-rich compounds such as proteins and lipids (Talbot 2001).

Fossil pigment concentrations are also likely to be affected by diagenesis during sinking and after burial (Leavitt 1993). The excursions in chlorophyll-*a* to pheophytin-*a* ratios in the most recent ~ 3.5 years of our core suggested that changes observed in the fossil carotenoids during that same period were due to diagenetic factors. Morever, the general decrease in the magnitude and variability of the chlorophyll-*a* / pheophytin-*a* ratio with depth in our 25 cm core suggested that some progressive degradation of fossil pigments occurred. However, the values were low suggesting that significant degradation had already occurred (*e.g.* during sinking), and the downcore changes were minor compared to the changes in the actual fossil pigment concentrations. Furthermore, we considered only organic-matter-specific pigment concentrations in our analysis (nmol g^{-1} organic matter) – a measure which can compensate for diagenetic losses where fossil

pigments co-vary with organic matter (Leavitt 1993). And finally, the exclusion of the more labile chlorophylls and pheophytins from our analysis was a further safeguard against the possibility that the observed recent increases in fossil carotenoid concentrations in our core were due only to pigment degradation.

The lack of discernable seasonal variation in the sedimentary $\delta^{13}C$ of Kitlope Lake suggested that this measure was robust to seasonal changes in organic matter concentration, as well as to changes in C/N and $\delta^{15}N$, both of which exhibited considerable seasonal variation. Indeed, sedimentary organic $^{13}C/^{12}C$ ratios have been shown to be far less prone to changes over time than organic C/N and $^{15}N/^{14}N$ ratios, even if substantial proportions of the associated organic matter are lost through diagenesis (Hodell and Schelske 1998). The lack of seasonal variation in $\delta^{13}C$ therefore suggests that photosynthetic CO_2 demands during past growing seasons were likely not sufficient to lead to season-dependent discrimination of the heavier isotope by primary producers, a common phenomenon in more productive and stratified lakes (Meyers and Teranes 2001 and references therein). Obviously we would not expect CO_2 limitation to occur in Kitlope Lake given its extremely low trophic status and weak thermal stratification. Therefore, the sedimentary $\delta^{13}C$ measured in this study was likely indicative of organic matter source (i.e. algal versus terrestrial) rather than seasonal CO_2 limitation. Indeed, lake algae have been shown to have significantly lower $\delta^{13}C$ values than terrestrial particulate organic matter in arctic lakes (Kling *et al.* 1992) and in the upper Kitlope River where the $\delta^{13}C$ of perphytic algae ($\bar{x}$ = -32.70 ‰ ± 5.08 std.dev.) is substantially lower than the foliar $\delta^{13}C$ of the dominant riparian deciduous trees and shrubs ($\bar{x}$ = -28.97 ‰ ± 1.71 std.dev.) (SaRON unpublished data). Moreover, this would explain why Kitlope Lake sedimentary $\delta^{13}C$ was negatively correlated with fossil carotenoids. The decreasing trend in $\delta^{13}C$ over time, coupled with the decreasing organic C/N and increasing TN and TOC, is therefore indicative of increasing aquatic organic matter and/or decreasing terrestrial organic matter contributions to sediments in Kitlope Lake.

Possible explanations for observed trends: climate warming, terrestrial N cycling and export

Concentrations of TN, TOC, $\delta^{15}N$, and fossil pigments increased sharply near the top of the core despite some of the lowest sockeye returns on record. In addition to being enriched by salmon-derived MDN, many other factors could have caused the recent increases in these proxies. As described above, incomplete degradation of sediment organic matter is a likely possibility (Leavitt 1993; Hodell and Schelske 1998; Talbot 2001). Another possibility is an undocumented increase in coho and/or chinook escapements to the Tezwa watershed. However, it is be difficult to evaluate this possibility due to the lack of reliable escapement estimates for those species compared to sockeye. Escapement estimates for chinook in the lower Kitlope River have led to conservation concerns in the past few years (Dave Peacock, DFO, pers.comm.) so it is unlikely that spawning populations of chinook in the Tezwa River, just a few kilometres upstream, have increased in recent years. Coho escapements on the other hand have increased in several north coast systems after reaching record low numbers in the late 1990s (Riddell 2004), and anecdotal accounts suggest that Kitlope coho escapements have also increased somewhat since the late 1990s (A. Hill pers. obs.). However, even with the recent increases, the numbers of coho spawning upstream of Kitlope Lake have not outnumbered sockeye, which have been at near-record lows. It is therefore unlikely that increased numbers of spawning coho would have provided high enough concentrations of MDN to Kitlope Lake to cause the recent observed increases in the productivity proxies.

In the case of $\delta^{15}N$, increased N cycling generally leads to elevated $\delta^{15}N$ through the influence of N-limitation and isotopic fractionation. Algae discriminate strongly against the heavier isotope when N is not limiting, but as ^{14}N is preferentially removed from the dissolved inorganic nitrogen (DIN) pool the $\delta^{15}N$ of settling algae will eventually approach the $\delta^{15}N$ of the bulk DIN as N-limitation increases (Teranes and Bernasconi 2000). Additional fractionation and organismal ^{15}N enrichment occurs at successive trophic transfers as the weaker-bonding ^{14}N is preferentially excreted by consumers through metabolic deamination (Talbot 2001). In the case of Kitlope Lake sediments it is unlikely that N-limitation was responsible for recently elevated $\delta^{15}N$,

based on the high aquatic molar N:P ratios we measured in 2005 (given above). Moreover, the extremely low average sedimentary $\delta^{15}N$ underscores the likelihood of chronic P-limitation in Kitlope Lake.

We established that average daily water and air temperatures in Kitlope Lake were significantly correlated with average daily air temperature measurements at the Environment Canada weather station in Kemano where daily temperature and precipitation measurements have been recorded since 1951. Mean annual air temperatures showed a clear warming trend over the period of record that was significantly correlated with the PDO, and the warming trend was particularly apparent from c.1972-2006.

Interviews with local Haisla and non-Haisla people provided compelling testimony indicating that freezing of the freshwater lens in Gardner Canal has become much less frequent in recent years, with sustained whole-Canal freeze-ups not occurring since the 1970s, and freeze-ups of smaller patches around Kemano not occurring in the past 6 years. We inferred from these findings that there has likely been an increasing trend in the annual ice-free period for Kitlope Lake, as well as increased aquatic and terrestrial primary production due to longer and warmer growing seasons. An increase in 2005 average chlorophyll-*a* concentrations over most values measured in weekly sampling during the first two years of the lake enrichment program (1979-80; Table 1) supports this idea.

Climate indicators (air temperature and/or PDO) and most of the sedimentary proxies (TN, $\delta^{15}N$, $\delta^{13}C$, and/or carotenoids) were significantly correlated, with the coherence between mean annual air temperature and $\delta^{15}N$ being particularly consistent over the period of record. These relationships demonstrate that climate has likely exerted significant control over the trophic status of Kitlope Lake from year to year and could partially explain why the $\delta^{15}N$ and salmon escapement trends decoupled in the early-mid 1970s, when the warming phase began and sockeye escapements were declining. The fact that $\delta^{15}N$ was increasing in the absence of N-limitation is explained by the fact that $\delta^{15}N$ is enriched by up to 4 ‰ in organisms at successive trophic transfers (DeNiro and Epstein 1981) which were likely increasing with climate-forced trophic status in Kitlope

Lake. This line of reasoning addresses the increasing trends in TN, $\delta^{15}N$ and carotenoids as well as the strong correlation between temperature and $\delta^{15}N$.

The trends observed in sedimentary proxies from Kitlope Lake are generally consistent with trends observed in other systems that were correlated with pollen-inferred climate-induced range expansion of alder (*Alnus* spp.) in the late Holocene. Through a symbiotic relationship with root-bound Actinomycetes (filamentous bacteria), pure stands of red alder (*Alnus rubra*) can fix atmospheric nitrogen at rates of up to 200 kg N ha^{-1} $year^{-1}$ (Binkley *et al.* 1994). The presence of alder can greatly increase primary productivity and N cycling in forest soils (Binkley *et al.* 1992) and nitrate leaching from red alder stands can exert strong controls on N export in coastal temperate watersheds (Compton *et al.* 2003).

Paleolimnological studies using *in situ* pollen grains have shown significant range expansion by *Alnus* spp. in the late Holocene in Alaska in response to climate change (e.g. Hu *et al.* 1995). The Kitlope Lake catchment has abundant nitrogen-fixing red alder (*Alnus rubra*) that likely supply several tonnes of nitrate to Kitlope Lake annually (Figure 10). Studies examining recent trends in alder growth in relation to climate change are rare for coastal British Columbia; however, Holtham *et al*. (2004) found a pronounced and sustained increase in the relative abundance of *Alnus* pollen grains in lake sediments beginning in the mid-1960s at Hobiton Lake on Vancouver Island, BC. Hu *et al*. (2001) found that pollen-inferred alder colonization of a lake catchment in southwestern Alaska 8000 years ago was associated with strong increases in both aquatic primary productivity inferred from biogenic silica and N-cycling inferred from a strong increase in $\delta^{15}N$. They also found that increased primary productivity was consistent with increased TN and TOC, decreased organic C/N, and decreased $\delta^{13}C$ – the same trends we observed in the Kitlope Lake core, albeit over a much shorter time scale. The recent increases in average annual temperatures in the Kitlope watershed have likely led to increased N-fixation and subsequent DIN export to Kitlope Lake from the abundant alder in its expansive drainage basin. However, further studies, such as time-series analyses of remotely sensed imagery or sedimentary pollen, would be necessary to ascertain the extent to which this has occurred.

Rain contains substantial amounts of DIN, and atmospheric nitrogen deposition may have contributed to the increases in sedimentary TN and $\delta^{15}N$ observed in this study. It is widely recognized that human activities such as fossil fuel burning have led to continually increasing inputs of nitrogen to the land, water, and air globally (Vitousek *et al.* 1997). In western North America, studies of both populated and pristine watersheds in the U.S. Rocky Mountains have demonstrated significant increasing trends in atmospheric deposition of inorganic nitrogen (Lehmann *et al.* 2005; Ellis 2006). However, extensive surveys of Scandinavian lakes have demonstrated that the intensity of atmospheric N deposition is strongly tied to distance from sources of emission with pristine areas showing little effect (Bergström *et al.* 2005). Extensive paleolimnologic studies of Svalbard lakes found no evidence that atmospheric N deposition was responsible for recent proxy-inferred increases in primary production, and suggested that the most likely culprit was changes to hydrologic and chemical processes through climate change (summarized in Birks *et al.* 2004).

We are not aware of any recent studies in central or north coastal British Columbia that have analyzed trends in atmospheric N deposition or that have estimated the fraction of bulk lake DIN that would be contributed by atmospheric sources. Analyses of the $\delta^{15}N$ of atmospheric DIN are few and geographically irrelevant for the purposes of this study. The possible range of values is quite high (-18 – +4 ‰) but averages from sites in close proximity to one another are typically negative (Talbot 2001 and references therein). Given the existing data and the remote location of the watershed, it is likely that atmospheric N inputs to the Kitlope have increased in recent years, but are not likely to be a dominant factor in the recent changes observed in Kitlope Lake. However, the paucity of locally-relevant research on this subject and the possible implications of even small increasing trends make it a priority for further study.

Summary, conclusions, and recommendations

Salmon in the Kitlope watershed were an important food source for the Haisla and Henaaksiala people for centuries and have supported commercial fisheries since the late 1800s. Average sockeye escapements to the Kitlope watershed prior to about 1950 were consistently about an order of magnitude higher than they have been in recent years. Kitlope sockeye have not met target escapements with any consistency for over 3 decades, and have been declining every brood year cycle since c.1986.

Over the period of record covered by this core Kitlope Lake sockeye dynamics were controlled by both climate and harvest. Local climate records were significantly correlated with large scale climatic trends in the North Pacific Ocean (i.e. PDO) and Kitlope sockeye escapements were significantly correlated with local temperature trends. Historically the commercial fishery intercepted substantial quantities of Kitlope sockeye and, although recent catches have declined along with escapements, an undetermined proportion of the Kitlope sockeye run is still intercepted every year in the mixed-stock harvest.

The paleolimnology of Kitlope Lake was dominated by its main tributary, the glacially turbid Tezwa River, as indicated by the extremely high sedimentation rate, substantial contributions of terrestrial organic material, and the dominance of periphytic algae. However, sedimentary $\delta^{15}N$, organic C/N, and fossil carotenoids all indicated that order-of-magnitude fluctuations in sockeye spawner densities significantly altered the trophic status of Kitlope Lake since c.1958. This was especially the case prior to c.1975, when sockeye escapements reached near-record lows and the PDO shifted (~ 1976) from a warming phase to a cooling phase. Around this time the trends in sedimentary $\delta^{15}N$, organic C/N, and fossil carotenoids decoupled from sockeye escapements while climate remained significantly correlated with proxy-inferred lake trophic status.

A distinct warming trend in the area over the 1952-2007 period of record was inferred from LTEK to be associated with an increased growing season and increasing ice-free period on Kitlope Lake since the mid-1970s PDO shift, and especially in the past 6 years. Recent increases in productivity proxies were likely partly due to diagenetic effects. However, the strong correlation between 1^{st}-differenced $\delta^{13}C$ and carotenoids and

the sharp increase in recent temperatures suggested that recent increases in TN, TOC, $\delta^{15}N$, and carotenoids, and decreased organic C/N and $\delta^{13}C$, were partly due to increased algal production. This was likely due to increased nutrient cycling caused by a longer growing season and/or increased non-salmon N inputs to the watershed. Comparisons with paleolimnological studies from other systems suggested that increased nitrate leaching from upstream N-fixing alder stands due to increased air temperatures may have also been partially responsible for the proxy-inferred increasing algal productivity in Kitlope Lake. Atmospheric N deposition from anthropogenic sources may have also contributed to observed sedimentary N increases; however, we are not aware of any region-specific analyses of atmospheric N sources that we could use to refute or substantiate this suggestion. This should therefore be a priority for future research along with paleoecological studies of nitrogen fixation and export by alders in relation to recent climatic change.

Although lake productivity and sockeye smolt sizes increased precisely at the time the lake fertilization program began, the response also appeared to be concomitant with the warming trend and increasing lake trophic status inferred from the lake core. The prevalence of periphytic diatoms in Kitlope Lake, presumably washed in from the Tezwa River, underscores the importance of watershed-wide nutrient cycling processes to the ecology of downstream nursery lakes in fast-flushing ultra-oligotrophic systems. Superficial nutrient applications may underestimate this importance.

This study demonstrated that lake coring may be a useful method to estimate past salmon escapements in fast-flushing ultra-oligotrophic glacial sockeye nursery lakes. Differences in lake area to catchment area ratios and related upstream MDN cycling may explain why correlations were not found between sockeye escapements and $\delta^{15}N$ in other fast-flushing sockeye nursery lakes in BC and Alaska. In any case, multi-proxy approaches are required to tease out the salmon signal from terrestrial and climate signals. To this end, isotopic and quantitative analyses of terrestrial, atmospheric, and internal N sources, along with remote sensing and paleolimnological analyses of watershed vegetation and glacier dynamics, could be of great value in future studies of sockeye nursery lakes.

Our results support previous assertions by others that salmon are generally underescaped in the Kitlope watershed, and show that escapements have been reduced to the extent that lake trophic status has likely come to be regulated by climate-related factors other than salmon-derived MDN. However, while climate warming may be partially mitigating productivity loss due to reduced MDN inputs from salmon, the system remains ultra-oligotrophic and apparently P-limited, and sockeye escapements to Kitlope Lake have declined to near-record lows in recent years. A substantial increase in annual sockeye escapement is required in this system in order to alleviate nutrient limitation and fully utilize the abundant rearing habitat.

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Appendix A: Local trends in salmon abundance and harvest and climatic conditions from LTEK and archival sources

Introduction and methods

This appendix is a synopsis of local and traditional ecological knowledge (LTEK) and anthropological discourse pertinent to the core study. Summaries fall into two broad categories: those from semi-directed interviews (Huntington 2000) conducted by A. Hill between December 2005 and March 2007 and those from previously published accounts and archival sources. All of the Haisla interviewees have extensive first-hand and hereditary (traditional) knowledge of the Kitlope and Gardner Canal area, as well as first-hand experience in the commercial fishing industry. With the exception of Glen Smith, all of them return to the Kitlope watershed every summer for subsistence fishing and other activities.

The interviews were broad in scope. Participants were asked questions regarding their memories around fisheries and population dynamics of salmon (*Oncorhynchus* spp.) and oolichan (*Thaleichthys pacificus*), and to a lesser extent Pacific herring (*Clupea pallasii*) within Haisla traditional territory. Interviewees were particularly encouraged to share their knowledge regarding sockeye fishing in Gardner Canal, population dynamics of Kitlope sockeye, climate dynamics and effects of ice cover, historic (pre-contact) Haisla demographics, the story of the Price and Co. salmon cannery (Kitlope estuary 1890-1893), opinions regarding resource management, and general Haisla lore and *nuyem* (traditional oral law). A wealth of fisheries-related narratives and observations and other traditional ecological knowledge was shared by the interviewees. However, for the sake of brevity only information deemed pertinent to the present study is included in this synopsis. Two non-Haisla individuals were also interviewed owing to their relevant first-hand observations of climate-related trends in the area.

The reader should note that several epidemics since the time of European contact decimated the Haisla (Kitamaat) and Henaaksiala (Kitlope) populations (described in more detail below). The epidemics, coupled with Henaaksiala emigration from the Kitlope to Kitamaat, eventually lead to the amalgamation of the two nations as Haisla in

1949 (Pritchard 1977). As such, the terms Haisla and Henaaksiala should be considered to be interchangeable only after the amalgamation.

Interviewees

JW: John Wilson (Chief Sunahead – Haisla elder), Kitamaat Village, BC

BW: Beatrice Wilson (Haisla elder), Kitamaat Village, BC

KH: Ken Hall (Chief C'ekwikas – Haisla elder) , Kitamaat Village, BC

CP: Cecil Paul Sr. (Wahxed – Haisla elder), Kitamaat Village, BC

GA: Gerald Amos (Ga Gaum Guist – Haisla elder), Kitamaat Village, BC

GS: Glen Smith (Haisla elder), Kitamaat Village, BC

DN: Dave Newman (Helicopter pilot, Canadian Helicopters, approx. 35 years experience flying helicopters in the Gardner Canal area year-round), Terrace, BC

GK: Graham Kerr (Ferry captain, Alcan Inc., 11 years experience making weekly boat trips between Kitimat and Kemano, BC), Terrace, BC

Henaaksiala demographics before and after European contact

Prior to the arrival of Europeans, the Northwest Coast of North America was one of the most densely populated non-agricultural regions in the world. Within a hundred years after European contact, smallpox and a host of other diseases reduced the Northwest Coast population from appox. 200 000 in 1774 to less than 40 000 by 1874 (Boyd 1990). Stable isotope analyses ($\delta^{13}C$) of human remains from multiple sites on the BC coast show that appox. 90 % of protein in pre-historic diets was of marine origin (this includes anadromous salmon and oolichan)(Chisolm *et al.* 1983), and archaeological surveys of ancient village sites show that salmon were often a primary food source (Ames 2003), with the oil-rich sockeye and chinook being particularly favoured (Yang *et al.* 2004; Speller *et al.* 2005). Coastal First Nations employed a variety of highly efficient capture and preservation techniques and in many cases exploitation rates were believed to rival those of modern industrial fisheries (Glavin 2000 and references therein).

The Haisla and Henaaksiala oral histories denote a strong and ancient dependence on salmon resources and salmon figure prominently in their mythologies (Barbetti 2005;

JW; unpublished Haisla arvhival notes). They employed numerous capture techniques including stone tidal pounds in the salt water and traps and weirs in rivers (Hamori-Torok 1990). The following summary of Henaaksiala and Haisla population demographics is presented to add some context for speculation on historic human exploitation of Kitlope Lake sockeye salmon.

The first confirmed European contact was by George Vancouver's expedition in June 1793. However, Jacinto Caamaño may have preceded Vancouver by about a year (Hamori-Torok 1990; BW). Estimates of pre-contact Henaaksiala populations for the Gardner Canal area range widely from < 800 (Boyd 1990) to > 3000 (KH, GA). A smallpox epidemic some time in the 1770s is known to have caused widespread mortality throughout the coastal First Nations. Conservative estimates put the coast-wide death toll at 30 % but the mortality occurred unwitnessed by Europeans, and the actual death toll could have been much higher (Boyd 1990). The Haisla and Henaaksiala appear to have been spared from the 1862-1863 smallpox epidemic that ravaged the rest of the north and central coast First Nations (Boyd 1990), but they were hit hard by numerous other epidemics including other smallpox epidemics, tuberculosis, and the influenza epidemic of 1917-18. Bureau of Indian Affairs census reports show the Henaaksiala population falling from 97 people in 1892 to 70 people in 1907, and the decline is generally attributed to tuberculosis and a low birth rate. Regarding the flu epidemic, one well-known narrative, recorded in unpublished Haisla archival notes, is particularly chilling:

> "During the flu epidemic of 1917-18 they'd ring the firehall bell every time someone would die. That bell never stopped ringing toward the end. The grave diggers were falling down tired. There was a lineup of people waiting to ring the bell."

The Kitlope people originally occupied several seasonal clan villages around Kitlope Lake and throughout the lower Kitlope River, and a few permanent villages including one near the Kitlope Lake outflow (BW) and Miskusa, at the estuary. However, as mentioned above the Henaaksiala people were eventually so few that they merged with the Haisla in 1949, and no longer took permanent residence in the Kitlope watershed. The above human population estimates suggest that the Kitlope sockeye population supported annual harvest levels of several thousand fish annually. For example, a conservative estimate of 1000 people consuming 10-15 sockeye each annually would put

harvest levels within the range of those from commercial fisheries in the past decade, but lower than harvest levels from earlier in the 20th century (Figure 2).

Salmon population and fishery dynamics

There is general agreement among the Haisla interviewees that salmon abundance in the Gardner Canal area has generally declined over their lifetimes, although there are mixed beliefs regarding the cause(s) of the declines. When asked specifically about trends in Kitlope sockeye, CP described recent returns as being "almost down to zero" compared to those in his youth, and GS stated that these runs had become "a lot smaller…*a lot*" over his lifetime with the most recent years being the worst. CP described the Kitlope River one year when he was a young man as being "so plugged up with sockeye you could walk across it". GA relayed observations from others describing the shores of Kitlope Lake as "solid red" with spawning sockeye in earlier decades. In contrast, lake-wide shore spawner counts from 2004-2006 did not exceed mean values of ~100 fish per linear km (A. Hill pers. obs.).

The Price and Co. cannery at Wakasu (a.k.a. Price Creek – near the Kitlope estuary) operated from 1890-1893 with annual packs averaging 422935 lbs, with most or all of it likely being sockeye (Lyons 1969; Pritchard 1977; Argue and Shepard 2005; unpublished Haisla archival notes). The fact that the cannery only operated for four years initially led us to suspect that the cannery may have over-exploited the sockeye run, leading to poor returns after the first full sockeye brood cycle. However, it appears that other factors led to the demise of the cannery. In describing the short-lived Price and Co. cannery at Wakasu, KH stated that "they tried canning there for a while, but then they backed out. There was a lot of fish there, for a start…lots…but it wasn't the commercial fishing that killed it." This claim is substantiated by other authoritative Haisla elders in unpublished Haisla archival notes and by industry insiders in Newell (1989): the cannery was severely damaged on two occasions from the catastrophic draining of an ice-dammed lake in Price Creek above the cannery, and when a barge carrying materials to rebuild the cannery capsized on the coast near Klemtu it was finally abandoned.

Additional knowledge of Kitlope salmon populations and fishery dynamics is sparse, especially from the period prior to the flu epidemic of 1918. However there is no

doubt that Kitlope sockeye were a key food item for the Henaaksiala prior to European contact. A former settlement on the lower Kitlope River near the mouth of Kitlope Lake had the name *Xwelxweltilalis*, meaning 'fire-on-the-ground place', for the red glow the gravel bar had from a distance when it would be covered in racks of red sockeye flesh drying in the sun (unpublished Haisla archival notes).

Table A1. Pack records from the Price and Co. cannery which operated near the Kitlope Estuary from 1890-1893 (Lyons 1969). Estimated equivalent fish numbers are based on industry standard conversion factors and an assumption that sockeye comprised 90 – 100 % of the pack (Argue and Shepard 2005; unpublished Haisla archival notes).

Year	Cases (48 x 1 lb. cans)	Lbs.	Equivalent green landed weight (GLW) (lbs. * 1.75)	Approx. no. sockeye (GLW / ~8 lbs.)
1890	3719	178512	312396	39000
1891	3876	186048	325584	41000
1892	6156	295488	517104	65000
1893	6484	311232	544656	68000

Until 1955 targeted commercial fisheries were conducted at the mouth of Gardner Canal (seine) and in the Canal itself (gillnet). Conservation concerns for numerous local stocks, including Kitlope sockeye, lead to a moratorium on these fisheries in 1955 that has never been lifted (CP; GA; JW; DFO Area History reports). Since then, the fishery has been conducted primarily in the coastal approach waters to Douglas Channel and Gardner Canal (i.e. W and NW of Butedale in Figure 1B).

Narratives from about the 1920s and on describe heavy harvest levels of Kitlope-bound sockeye in the commercial fishery. The earliest accounts were relayed by GA. His uncle noted from reading log books at the Butedale cannery in the 1920s and 30s that seiners would catch up to 20 000 sockeye in single sets near Crab River at the entrance to Gardner Canal (Figure 1), deliver the fish to the cannery, and return for another equivalent set in the same day. A more recent account from the early 1980s described the effect of a commercial fishing closure on subsistence fishing success. GA and his fishing partner Cyril Grant observed a ~ 1 km^2 school of sockeye near Collins Bay (~ 5 km south of Crab River) from which they instantaneously caught 400 fish using 35 fathoms (64 m) of gillnet. GA described the water as being "solid black with sockeye" and stated that it was the largest school of sockeye either of them had ever seen. The reason for this

commercial fishery closure, its exact year, and its duration are unclear. In any case, Kitlope sockeye run is typically 1-2 orders of magnitude larger than any other sockeye run in the region, so the fish caught in the above narratives were most likely Kitlope-bound.

Climate dynamics

There was a common belief among the interviewees, supported by first-hand observations, that there has been a warming trend in the area over their lifetimes. Direct observations of the duration of ice cover on Kitlope Lake were not available, as Kitlope Lake was generally not inhabited during the winter months when families would reside at Miskusa (Kitlope estuary) and Kemano Beach. However, the fresh water lens on Gardner Canal regularly freezes during winter cold snaps and is known to have frozen over solid many winters as far out as Brim River (JW; CP; KH; GS; GA; GK; DN; unpublished Haisla archival notes; Figure 1B). Observations on the frequency and duration of these winter freeze ups are a suitable proxy for ice cover on Kitlope Lake due to its close proximity and shared weather patterns with Gardner Canal (Figure 3, Figure 4). For example, KH remembers trapping with his father around Kitlope Lake as a boy and having to suddenly flee the watershed when a heavy snowfall began freezing on the lake surface and nearly immobilized their outboard-powered canoe. Once past the estuary, they encountered similar conditions in Gardner Canal, and took nearly 4 hours to motor 25 km to Chief Matthews Bay breaking their way through the slush-ice with paddles. Sometime in the 1920s the water froze from Kitlope Lake, down the lower Kitlope River, and out to Brim River and the late Gordon Robertson fashioned a sled out of a canoe with yellow cedar runners and a mast and sail to make the voyage while a steamship waited for him at the edge of the ice for 3 days (unpublished Haisla archival notes). The Alcan corporation has used tugboats and dynamite on several occasions to break the ice for their other vessels not designed to withstand ice-breaking (GK; CP).

In making regular helicopter trips to Kemano since the early 1970s DN has observed Gardner Canal frozen over on several occasions, but has not seen a solid freeze-over out to Brim River since the 1970s. In making weekly boat trips to and from Kemano

over the past 11 years GK has seen Gardner Canal frozen over approx. 1 in. (2.5 cm) thick “about a half dozen times” but has generally seen much less ice in the past 6 years. CP stated that the last time he had heard of Gardner Canal freezing over completely was around 1939 (JW witnessed it in the early 1940s frozen solid out to Brim River), and that since then portions of the Canal have frozen over “but not the whole thing”. CP, who was born and raised in the Kitlope watershed, recalled traveling as a boy with his father upriver to one of the glaciers that feeds the mainstem Kitlope River. In a recent helicopter overflight he noted that the same glacier was about half the size that it had been when he saw it as a boy.

Consolidated snow pack in slide chutes near the Kitlope estuary and sometimes along the shores of Kitlope Lake provide a convenient source of ice in the summer months, and sometimes year-round (Figure A1). In recent years this ice has been less abundant and has retreated earlier making it difficult to access, especially during the sockeye subsistence fishing season (August) when it is coveted for preserving catches (CP; GA). Related, JW noted that when he was a child there would regularly be shore ice in front of Kitamaat Village (brackish water) during the winter, but this is a rare occurrence nowadays. Regarding the record snowpack delivered to the BC northern coast mountains during the winter of 2007, CP remarked that “there’s lots of snow this year, but it’s all up high, there’s none down at the water line”, which would have been expected in previous decades.

Figure A1. Collecting ice (consolidated snow) from a slide chute in Gardner Canal approx. 5 km from the Kitlope estuary on June 20, 2005. Photograph was taken from a boat at sea level.